

Bibliography on CO₂ Effects on Vegetation and Ecosystems: 1990-1999 Literature

Michael H. Jones and Peter S. Curtis, editors

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1

Abarzua, S., R. Altenburger, R. Callies, L.H. Grimme, A. Mayer, D. Leibfritz, and U. Schiewer. 1993. Ammonium rhythm in cultures of the cyanobacterium *Microcystis- firma*. *Physiologia Plantarum* 89(3):659-663.

Over a period of several days, rhythmic changes in extracellular NH₄⁺ concentration take place in cultures of the cyanobacterium *Microcystis firma* (Breb et Lenorm.) Schmidle, strain Gromov/St. Petersburg. 398, under conditions of restricted CO₂ supply and light/dark alternation. The changes are enhanced by nitrate supply. Among the various processes generating intracellular NH₄⁺ (NH₄⁺ uptake, NO₃⁻ reduction, protein and amino acid degradation, photorespiration), NO₃⁻ reduction appears as the one most important. This can be concluded from experiments with and without nitrate and/or ammonium in the medium. In the presence of saturating CO₂, continuous light, or continuous darkness, rhythmic NH₄⁺ oscillations are not induced. Studies of the incorporation of NH₄⁺ nitrogen by in vivo N-15-NMR show that if CO₂ is supplied, N-15 is accumulated in several components with the following time course: in the first hour in Gln (delta), in the second hour in the alpha- amino groups of most nonbranched amino acids, in the third hour in gamma-aminobutyric acid (GABA), Orn (delta) and Lys (epsilon), and in the sixth hour in Ala. Carbon limitation, however, results in accumulation of label in the amide nitrogen of glutamine only.

KEYWORDS: METABOLISM, N-15, NMR-SPECTROSCOPY, NUCLEAR MAGNETIC-RESONANCE

2

Abdin, O.A., X.M. Zhou, B.E. Coulman, D. Cloutier, M.A. Faris, and D.L. Smith. 1998. Effect of sucrose supplementation by stem injection on the development of soybean plants. *Journal of Experimental Botany* 49(329):2013-2018.

Over the past half decade several stem injection methods have been developed for cereal plants. These methods allow researchers to administer solutions to cereal plants to study their effects on plant physiology. However, little work has been done to extend this technique to non-cereals. An experiment was conducted to test an injection technique that could be suitable for soybean plants (*Glycine max* [L.] Merr.), and to study the effect of long-term injection of sucrose on the growth of soybean plants. An injection setup comprising a supporting stand and a fluid injection system was established. Pressure was applied to the plunger of a 5 ml syringe using ceramic bricks to force test solutions into the plants. Solutions of 0, 150, and 300 g sucrose I-1 were injected into soybean plants for 8 weeks starting at the seedling VC stage. Distilled water had the greatest uptake rate, followed by the 150, and then the 300 g sucrose I-1 solutions. The overall average uptake

during the injection period was 77.3 ml. Average sucrose uptake values were 11.8 and 13.5 g per plant for the 150 and 300 g sucrose I-1 treatments. This represented approximately 65% of the total dry weight of the plants. Sucrose injection increased leaf area and pod number relative to the control plants. Nodule numbers were lower for sucrose injected treatments, but their dry weights were higher than the control. Above-soil dry matter was higher for the plants injected with 300 g sucrose I-1 than those injected with water. The injection system tested was able to administer concentrated solutions into soybean plants for most of their period of growth and development. The sucrose supplementation had positive effects on soybean growth but suppressed photosynthesis.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, GROWTH, LEAVES, MAIZE, NITROGEN, PEDUNCLE PERFUSION, PHOTOSYNTHESIS, WHEAT, YIELD

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Abdullaev, A.A., B.B. Dzhumaev, Z.N. Abdurakhmanova, V.L. Kaler, and I.M. Magmedov. 1992. Integral effect of environmental-factors on photosynthetic metabolism of carbon in cotton leaves. *Soviet Plant Physiology* 39(2):140-144.

We used the method of mathematical experiment planning (a 2(3) scheme) to study the influence of environmental factors separately or in combination on the photosynthetic rate and distribution of C-14 among products of photosynthetic carbon metabolism in the cotton (*Gossypium hirsutum* L.) leaf. Increase of light intensity during cultivation accelerated photosynthesis and stimulated incorporation of C-14 into phosphoglyceric acid (PGA), sugar diphosphate (SDP), fructose monophosphate (FMP), and malate, but suppressed incorporation of C-14 into sucrose, glucose monophosphate (GMP), and glycerate. Temperature increase by itself and in any combination with other factors at the upper level suppressed photosynthesis. Elevated temperature increased accumulation of the label in PGA, sucrose, and malate, but lowered it in GMP, alanine, glycine, and serine. Growing plants at enhanced CO₂ concentration led to acceleration of photosynthesis and increase of the share of C-14 in SDP, GMP, and malate, but decrease of it in sucrose, alanine, glycine, and serine. Very perceptible effects of interaction are discernible in different combinations of factors. All three factors at the upper level appreciably induced activity of phosphoenolpyruvate carboxylase (PEPCase) in cotton leaves.

KEYWORDS: PHYSIOLOGY

4

Aben, S.K., S.P. Seneweera, O. Ghannoum, and J.P. Conroy. 1999.

Nitrogen requirements for maximum growth and photosynthesis of rice, *Oryza sativa* L-cv. Jarrah grown at 36 and 70 Pa CO₂. *Australian Journal of Plant Physiology* 26(8):759-766.

The hypothesis that growth of rice (*Oryza sativa* L. cv. Jarrah) at elevated atmospheric CO₂ partial pressure alters leaf nitrogen (N) concentrations required to support maximum dry mass production and photosynthetic rates during the period of rapid tiller initiation was tested by growing plants for 30 days in unstirred sand/hydroponic culture with N concentrations of 5, 20, 40, 60 and 100 mg N L⁻¹. Maximum growth and photosynthetic potential was greater at 70 than 36 Pa CO₂ at all N concentrations in the solution. Elevated CO₂ reduced leaf N concentrations required to support 90% of maximum growth and photosynthetic rates (critical concentration) from 40 to 27 g kg⁻¹ for growth and from 45 to 30 g kg⁻¹ for photosynthesis. Morphological changes at elevated CO₂ included increased tiller numbers and reduced leaf area ratio. The latter could be explained by lower plant N concentrations which occurred at high CO₂ at each N concentration in the solution, primarily due to lower leaf blade and root N concentrations. Changes in tiller numbers at high CO₂ were unrelated to leaf or plant N but were strongly correlated with leaf soluble carbohydrate concentrations. We conclude that elevated CO₂ alters the nutritional physiology of rice during the rapid tillering phase in a way that increases the efficiency of N utilisation for growth and photosynthesis.

KEYWORDS: ACCLIMATION, CAPACITY, COTTON, ELEVATED CO₂, LEAVES, NUTRITION, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, WHEAT

5

Aber, J.D., S.V. Ollinger, C.A. Federer, P.B. Reich, M.L. Goulden, D.W. Kicklighter, J.M. Melillo, and R.G. Lathrop. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5(3):207-222.

Rapid and simultaneous changes in temperature, precipitation and the atmospheric concentration of CO₂ are predicted to occur over the next century. Simple, well-validated models of ecosystem function are required to predict the effects of these changes. This paper describes an improved version of a forest carbon and water balance model (PnET-II) and the application of the model to predict stand- and regional-level effects of changes in temperature, precipitation and atmospheric CO₂ concentration. PnET-II is a simple, generalized, monthly time-step model of water and carbon balances (gross and net) driven by nitrogen availability as expressed through foliar N concentration. Improvements from the original model include a complete carbon balance and improvements in the prediction of canopy phenology, as well as in the computation of canopy structure and photosynthesis. The model was parameterized and run for 4 forest/site combinations and validated against available data for water yield, gross and net carbon exchange and biomass production. The validation exercise suggests that the determination of actual water availability to stands and the occurrence or non-occurrence of soil-based water stress are critical to accurate modeling of forest net primary production (NPP) and net ecosystem production (NEP). The model was then run for the entire NewEngland/New York (USA) region using a 1 km resolution geographic information system. predicted long-term NEP ranged from -85 to + 275 g C m⁻² yr⁻¹ for the 4 forest/site combinations, and from -150 to 350 g C m⁻² yr⁻¹ for the region, with a regional average of 76 g C m⁻² yr⁻¹. A combination of increased temperature (+6 degrees C), decreased precipitation (-15%) and increased water use efficiency (2x, due to doubling of CO₂) resulted generally in increases in NPP and decreases in water yield over the region.

KEYWORDS: DEPOSITION, ECOSYSTEMS, ELEVATED CO₂, MODEL, REGIONAL-ANALYSIS, RESPONSES

6

Ackerly, D.D., and F.A. Bazzaz. 1995. Plant-growth and reproduction along CO₂ gradients - nonlinear responses and implications for community change. *Global Change Biology* 1(3):199-207.

The effects of rising atmospheric CO₂ concentrations on natural plant communities will depend upon the cumulative responses of plant growth and reproduction to gradual, incremental changes in climatic conditions. We analysed published studies of plant responses to elevated CO₂ to address whether reproductive and total biomass exhibit similar enhancement to elevated vs. ambient CO₂ concentrations, and to assess the patterns of plant response along gradients of CO₂ concentrations. In six annual plant species, mean enhancement at double ambient vs. ambient CO₂ was 1.13 for total biomass and 1.30 for reproductive biomass. The two measures were significantly correlated, but there was considerable scatter in the relationship, indicating that reproductive responses cannot be consistently predicted from enhancement of total biomass. Along experimental CO₂ gradients utilizing three concentrations, there was a great diversity of response patterns, including positive, negative, non-monotonic and non-significant (nat) responses. The distribution of response patterns differed for plants grown in stands compared to those grown individually. Positive responses were less frequent in competitive environments, and non-monotonic responses were more frequent. These results emphasize that interpolation of plant response based on enhancement ratios measured at elevated vs. ambient CO₂ concentrations is not sufficient to predict community responses to incremental changes in atmospheric conditions. The consequences of differential response patterns were assessed in a simulation of community dynamics for four species of annual plants. The model illustrates that the final community composition at a future point in time depends critically on both the magnitude and the rate of increase of atmospheric CO₂.

KEYWORDS: ANNUALS, ATMOSPHERIC CO₂, CO₂-INDUCED CLIMATE CHANGE, COMPETITION, ELEVATED CO₂, ENRICHMENT, LIQUIDAMBAR- STYRACIFLUA, OLD- FIELD PERENNIALS, PINUS-TAEDA SEEDLINGS, RESOURCE USE

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Ackerly, D.D., J.S. Coleman, S.R. Morse, and F.A. Bazzaz. 1992. CO₂ and temperature effects on leaf-area production in 2 annual plant-species. *Ecology* 73(4):1260-1269.

We studied leaf area production in two annual plant species, *Abutilon theophrasti* and *Amaranthus retroflexus*, under three day/night temperature regimes (18-degrees/14-degrees, 28-degrees/22-degrees, and 38-degrees/31-degrees-C) and two concentrations of carbon dioxide (400 and 700-μmol/L). The production of whole-plant leaf area during the first 30 d of growth was analyzed in terms of the leaf initiation rate, leaf expansion, individual leaf area, and, in *Amaranthus*, production of branch leaves. Temperature and CO₂ influenced leaf area production through effects on the rate of development, determined by the production of nodes on the main stem (the plastochron index), and through shifts in the relationship between whole-plant leaf area and the number of main stem nodes. In *Abutilon*, leaf initiation rate was highest at 38-degrees, but area of individual leaves was greatest at 28-degrees. Total leaf area was greatly reduced at 18-degrees due to slow leaf initiation rates. Elevated CO₂ concentration increased leaf initiation rate at 28-degrees, resulting in an increase in whole-plant leaf area. In *Amaranthus*, leaf initiation rate increased with temperature, and was increased by elevated CO₂ at 28-degrees. Individual leaf area was greatest at 28-degrees, and was increased by elevated CO₂ at 28-degrees but decreased at 38-degrees. Branch leaf area displayed a similar response to CO₂, but was greater at 38-degrees. Overall, whole-plant leaf area was slightly increased at 38-degrees relative to 28-degrees, and elevated CO₂ levels resulted in increased leaf area at 28-degrees but decreased leaf area at 38-degrees. The effects on leaf area closely parallel rates of biomass

accumulation in the same experiment, suggesting that responses of developmental processes to elevated CO₂ and interacting factors may play an important role in mediating effects on plant growth.

KEYWORDS: C-3, CANOPY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, GROWTH, LEAVES, LIGHT, PHOTOSYNTHESIS, RESPONSES, SUNFLOWER

8

Acock, B., M.C. Acock, and D. Pasternak. 1990. Interactions of CO₂ enrichment and temperature on carbohydrate production and accumulation in muskmelon leaves. *Journal of the American Society for Horticultural Science* 115(4):525-529.

9

Acock, B., and G.W. Wall. 1995. A simple conductimetric CO₂ analyzer with automatic recalibration .1. Design, implementation, and functionality. *Agronomy Journal* 87(1):70-75.

Controlled-environment plant growth cabinets may be used to investigate the long-term effect of elevated carbon dioxide concentration ([CO₂]) on plant growth. Infrared gas analyzers (IRGAs) are normally used to monitor and control [CO₂] in plant cabinets. With many cabinets in use, however, it soon becomes impractical to purchase an individual IRGA for each cabinet. A more economical method of monitoring and controlling [CO₂] relies on the change in electrical conductivity when CO₂ is dissolved in demineralized water. This work describes the design, implementation, and functionality of an inexpensive conductimetric system for controlling [CO₂] in plant growth cabinets. Regressing electrical conductivity against [CO₂] over the range 0 to 1000 $\mu\text{mol L}^{-1}$ yields a quadratic response. Calibration drift inherent in the conductimetric CO₂ analyzer requires that each analyzer be recalibrated periodically. Automatically recalibrating with an IRGA every 900 s gave control of the [CO₂] within the plant enclosures to within 10 to 15 $\mu\text{mol L}^{-1}$ of the set point. The [CO₂] control system is robust enough to maintain this accuracy regardless of the desired [CO₂] set point or the mass of plant material within the plant growth cabinet. In this approach, only one IRGA is required to control [CO₂] in many plant growth cabinets if each cabinet has a dedicated conductimetric CO₂ analyzer.

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Adams, R.M., R.A. Fleming, C.C. Chang, B.A. McCarl, and C. Rosenzweig. 1995. A reassessment of the economic-effects of global climate-change on US agriculture. *Climatic Change* 30(2):147-167.

This study uses recent GCM forecasts, improved plant science and water supply data and refined economic modeling capabilities to reassess the economic consequences of long-term climate change on U.S. agriculture. Changes in crop yields, crop water demand and irrigation water arising from climate change result in changes in economic welfare. Economic consequences of the three GCM scenarios are mixed; GISS and GFDL-QFlux result in aggregate economic gains, UKMO implies losses. As in previous studies, the yield enhancing effects of atmospheric CO₂ are an important determinant of potential economic consequences. Inclusion of changes in world food production and associated export changes generally have a positive affect on U.S. agriculture. As with previous studies, the magnitude of economic effects estimated here are a small percentage of U. S. agricultural value.

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Adamse, P., and S.J. Britz. 1992. Amelioration of uv-b damage under high irradiance .1. Role of photosynthesis. *Photochemistry and photobiology* 56(5):645-650.

Sensitivity to ultraviolet-B radiation (UV-B, 280-315 nm) is generally reduced when background irradiance is high. We tested the involvement of photosynthesis in the amelioration of UV-B damage by treating plants at high PAR (photosynthetically- active radiation. 400-700 nm; 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) with supplemental UV-B at double ambient levels of biologically- effective radiation (18 kJ $\text{m}^{-2} \text{d}^{-1}$) and either "ambient" (450 $\mu\text{mol mol}^{-1}$) or short term elevated (750 $\mu\text{mol mol}^{-1}$) CO₂ levels. Responses to UV-B were assessed by photosynthetic gas exchange, leaf expansion and production of UV-absorbing compounds (presumptive flavonoids) in cultivars of cucumber (*Cucumis sativus* L.) previously demonstrated to be relatively sensitive (cv. Poinsett) and insensitive (cv. Ashley) to UV-B. Except for marginal leaf interveinal chlorosis observed in Poinsett, both cultivars responded similarly. UV-B had little direct effect on leaf photosynthesis, but it did cause reductions in leaf area and corresponding increases in leaf dry matter per area. Increased CO₂ stimulated plant growth, counteracting the effect of UV-B on leaf growth and indicating an important role for photosynthesis. In contrast, the accumulation of UV-absorbing flavonoid compounds was enhanced by UV-B exposure but was not affected by CO₂ enrichment.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CELL-SUSPENSION CULTURES, LIGHT, PETROSELINUM- HORTENSE, PHOTON FLUX-DENSITY, PHYTOCHROME, PLANTS, RADIATION, SENSITIVITY

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Adamsen, F.J., P.J. Pinter, E.M. Barnes, R.L. LaMorte, G.W. Wall, S.W. Leavitt, and B.A. Kimball. 1999. Measuring wheat senescence with a digital camera. *Crop Science* 39(3):719-724.

Documenting crop senescence rates is often difficult because of the need for frequent sampling during periods of rapid change and the subjective nature of human visual observations. The purpose of this study was to determine the feasibility of using images produced by a digital camera to measure the senescence rate of wheat and to compare the results with changes in greenness determined by two established methods. Measurements were made as part of an experiment to determine the effects of elevated CO₂ and limited soil nitrogen on spring wheat (*Triticum aestivum* L.) at the University of Arizona's Maricopa Agricultural Center, near Phoenix, AZ. "Greenness" measurements were made during senescence of the crop with a color digital camera, a hand-held radiometer, and a SPAD chlorophyll meter. The green to red (GIR) for each pixel in an image was calculated and the average GIR computed for cropped images from a digital camera representing 1 m² for each treatment and sample date. The normalized difference vegetation index (NDVI) was calculated from the red and near-infrared canopy reflectances measured with a hand held radiometer. A SPAD reading was obtained from randomly selected flag leaves. All three methods of measuring plant greenness showed similar temporal trends. The relationships between GIR with NDVI and SPAD were linear over most of the range of GIR. However, NDVI was more sensitive at low values than GIR. GIR was more sensitive above G/R values of 1.2 than SPAD because the upper limits of SPAD measurements were constrained by the amount of chlorophyll in the leaf, while GIR responded to both chlorophyll concentration in the leaves as well as the number of leaves present. Color digital imaging appears useful for quantifying the senescence of crop canopies. The cost of color digital cameras is expected to decrease and the quality and convenience of use to improve.

KEYWORDS: CHLOROPHYLL METER, CROP, EFFICIENCY, RED, VEGETATION INDEXES, WINTER-WHEAT, YIELD

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Agar, I.T., J. Streif, and F. Bangerth. 1997. Effect of high CO₂ and controlled atmosphere (CA) on the ascorbic and dehydroascorbic acid content of some berry fruits. *Postharvest Biology and Technology* 11(1):47-55.

High CO₂ concentrations as well as controlled atmosphere storage are widely used to extend the storage and shelf-life of many fruits. To investigate the effect of these storage procedures on several berry fruits, strawberries, raspberries, currants and blackberries were stored at three different elevated CO₂ concentrations, with or without a parallel reduction in O₂. Vitamin C content (ascorbic acid plus dehydroascorbic acid) was reduced by high CO₂ concentrations (10-30% CO₂), particularly in strawberries. This reduction in vitamin C was moderate in black currants and blackberries and almost absent in raspberries and red currants when compared with strawberries. Reducing the O₂ concentration in the storage atmosphere in the presence of high CO₂ had little effect on the vitamin C content. Ascorbic acid was more diminished at high CO₂ than dehydroascorbic acid. This suggests a stimulating effect of high CO₂ concentrations on the oxidation of ascorbic acid and/or an inhibition of mono- or dehydroascorbic acid reduction to ascorbic acid. (C) 1997 Elsevier Science B.V.

KEYWORDS: HYDROGEN- PEROXIDE, O₂, PLANTS

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Aggangan, R.T., A.M. O'Connell, J.F. McGrath, and B. Dell. 1999. The effects of Eucalyptus globulus Labill. leaf litter on C and N mineralization in soils from pasture and native forest. *Soil Biology and Biochemistry* 31(11):1481-1487.

The effects of addition of Eucalyptus globulus leaf litter on carbon and nitrogen mineralization in soils from a pasture and a native forest were evaluated using a long-term laboratory aerobic incubation assay (29 weeks at 20 degrees C) in leaching microlysimeters. The amount of added leaf litter significantly influenced microbial respiration, microbial biomass and N turnover in both the native forest and pasture soils. Cumulative CO₂-C respired increased with increasing rate of leaf litter addition when leaf litter was mixed through the soil or placed on the soil surface. These increases were associated with increases in microbial biomass C content. Cumulative net N mineralization declined in all treatments when litter was added and was lowest when leaf litter was mixed with soil. When leaf litter was added in increasing amounts to the soil surface, there was a concomitant increase in microbial biomass N content ($r(2) = 0.79$, $n = 8$), indicating that the reduction in net N mineralization was primarily due to immobilization of N in microbial tissues. In contrast, when litter was mixed with soil in increasing amounts, there was a decrease in microbial biomass N in forest soil and an increase in pasture soil. Consequently, changes in the rate of net N mineralization were not well related to changes in microbial biomass N content. It is suggested that this may be due to the greater activity and more rapid turnover of microorganisms where litter was incorporated resulting in more of the immobilized N being partitioned into metabolic products or dead microbial cells. Incorporation of litter may also have enhanced loss N through denitrification. (C) 1999 Published by Elsevier Science Ltd. All rights reserved.

KEYWORDS: DECOMPOSITION, DENITRIFICATION, EXTRACTION METHOD, IMMOBILIZATION, LITTER, MICROBIAL BIOMASS CARBON, NITROGEN MINERALIZATION, PLANT RESIDUES, RESPIRATION, WESTERN-AUSTRALIA

15

Agren, G.I. 1996. Nitrogen productivity or photosynthesis minus respiration to calculate plant growth? *Oikos* 76(3):529-535.

One approach to calculate plant growth rate is from models of photosynthesis, respiration and allocation. This requires that processes with characteristic time constants of seconds to minutes be scaled to hours or days. Another approach is to use aggregate models defined at the time scale of growth, hours and days. I use such an aggregate model, the nutrient productivity, to compare the performance of the two approaches on growth experiments with small, nitrogen-limited birch plants. The problems of error aggregation when using the large number of parameters required to scale from the detailed level of photosynthesis and respiration to the aggregate level of growth are in this case such that whole plant growth rate is more accurately predicted with the nutrient productivity model.

KEYWORDS: ALLOCATION, BETULA-PENDULA ROTH, BIOMASS, BIRCH SEEDLINGS, CARBON, CLIMATE, ECOSYSTEMS, ELEVATED CO₂, NUTRITION, STRESS

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Agren, G.I., R.E. McMurtrie, W.J. Parton, J. Pastor, and H.H. Shugart. 1991. State-of-the-art of models of production decomposition linkages in conifer and grassland ecosystems. *Ecological Applications* 1(2):118-138.

We review the state-of-the-art of models of forests and grasslands that could be used to predict the impact of a future climate change arising from increased atmospheric carbon dioxide concentration. Four levels of resolution are recognized: physiologically based models, population models, ecosystem models, and regional or global models. At the physiological level a number of important processes can be described in great detail, but these models often treat inadequately interactions with nutrient cycles, which operate on longer time scales. Population and ecosystem models can, on the other hand, encapsulate relationships between the plants and the soil system, but at the expense of requiring more ad hoc formulations of processes. At the regional and global scale we have so far only steady-state models, which cannot be used to predict transients caused by climate change. However, our conclusion is that, in spite of the gaps in knowledge, there are several models based on dominant processes that are well enough understood for the predictions of those models to be taken seriously.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, BOUTELOUA-GRACILIS, CARBON DIOXIDE, CO₂-INDUCED CLIMATE CHANGE, EVEN- AGED STANDS, LOLIUM-PERENNE L, NITROGEN PRODUCTIVITY, PLANT GROWTH, SIMULATION-MODEL, THEORETICAL- ANALYSIS

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Ahmedi, H., W.V. Biasi, and E.J. Mitcham. 1999. Control of brown rot decay of nectarines with 15% carbon dioxide atmospheres. *Journal of the American Society for Horticultural Science* 124(6):708-712.

Effects of short-term exposure to a 15% CO₂ atmosphere on nectarines [Prunus persica (L.) Batsch (Nectarine Group) 'Summer Red'] inoculated with Monilinia fructicola (Wint.) Honey (causal agent of brown rot) were investigated. Nectarines were inoculated with spores of M.fructicola and incubated at 20 degrees C for 24, 48 or 72 hours and then transferred to storage in either air or air enriched with 15% CO₂ at 5 degrees C. Fruit were removed from storage after 5 and 16 days and were examined for brown rot decay immediately and after ripening in air for 3 days at 20 degrees C. Noninoculated nectarines were stored and treated likewise for evaluation of postharvest fruit attributes to determine their tolerance to 15% CO₂. Incubation period after inoculation, storage duration, and storage atmosphere had highly significant effects on fruit decay. 'Summer Red' nectarines tolerated a 15% CO₂ atmosphere for 16 days at 5 degrees C. Development of brown rot decay in fruit inoculated 24 hours before 5 or 16 days storage in 15% CO₂ at 5 OC was arrested.

After 3 days ripening in air at 20 degrees C, the progression of brown rot disease was rapid in all inoculated nectarines, demonstrating the fungistatic effect of 15% CO₂. The quantity of fungal cell wall materials (estimated by glucosamine concentration) was compared to visual estimation of decayed area and visual rating of fungal sporulation. The glucosamine assay defined the onset and progress of brown rot infection more precisely than either of the two visual tests.

KEYWORDS: FRUIT, IPRODIONE, MOLD, SUPPRESSION, SWEET CHERRIES, TISSUE, TOMATO PRODUCTS

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Ahmed, F.E., A.E. Hall, and M.A. Madore. 1993. Interactive effects of high-temperature and elevated carbon-dioxide concentration on cowpea [*Vigna-unguiculata* (L) walp]. *Plant, Cell and Environment* 16(7):835-842.

Limitations in carbohydrate supplies have been implicated as a factor responsible for reproductive failure under heat stress. Heat stress affects two stages of reproductive development in cowpea [*Vigna unguiculata* (L.) Walp.], and genotypes are available with tolerance and sensitivity to heat during these different stages. The objectives of this study were to determine the responses of these cowpea lines to ambient and elevated [CO₂], under heat stress and optimal temperature, and test whether differences in carbohydrate supplies due to genotypes, CO₂ enrichment and heat stress are associated with differences in sensitivity to heat during reproductive development. Plants were grown in reach-in growth chambers and subjected to day/night temperatures of either 33/20 or 33/30- degrees-C, and [CO₂] levels of either 350 or 700 mumol mol⁻¹. Under intermediate night temperature (33/20-degrees-C), all lines set substantial numbers of pods. Under high night temperature (33/30-degrees-C) with either ambient or elevated [CO₂], one heat-sensitive line produced no flowers and the other set no pods, whereas the heat-tolerant line abundantly set pods. High night temperature reduced the overall carbohydrate content of the plants, especially peduncle sugars, and caused decreases in photosynthetic rates. The high pod set of the heat-tolerant line, under high night temperature, was associated with higher levels of sugars in peduncles compared with the heat-sensitive lines. The heat-tolerant line accumulated substantial shoot biomass, exhibited less accumulation of starch in leaves, and possibly had less down-regulation of photosynthesis in response to CO₂ enrichment and heat stress than the heat-sensitive lines. Elevated [CO₂] resulted in higher overall carbohydrate levels in heat-sensitive lines (starch in leaves, stems and peduncles), but it did not increase their heat tolerance with respect to flower production or pod set. Heat-induced damage to floral buds and anthers in the sensitive lines was associated with low sugars levels in peduncles, indicating that heat had greater effects on assimilate demand than on leaf assimilate supply. The heat-tolerant line was the most responsive genotype to elevated [CO₂] with respect to pod production under either high or intermediate temperatures.

KEYWORDS: ABSCISSION, ACCLIMATION, AIR-TEMPERATURE, CO₂, COTTON, HEAT-STRESS, LEAVES, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, REPRODUCTIVE RESPONSES

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Aikman, D.P. 1996. A procedure for optimizing carbon dioxide enrichment of a glasshouse tomato crop. *Journal of Agricultural Engineering Research* 63(2):171-183.

The procedure consists of two parts. A Gompertz model for the kinetics of fruit growth is used to predict the time distribution of photosynthate subsequent harvests. This is combined with predictions of future market prices to compute estimates, one for each day from first anthesis, of a factor to convert CO₂ assimilate to expected financial value, based on the worth anticipated from partitioning to fruit. A model of the climate

and the crop regime is used to predict temperatures and hence allow for the temperature dependence of fruit growth. The conversion estimates are revised to include the deferred benefit given by additional photosynthesis through increasing early vegetative growth, and hence subsequent photosynthesis and yield. This revision also extends the set of conversion factors to include any period before first anthesis. Given the current environmental variables and conversion factor for that day, a real-time system can use a crop photosynthesis model to predict the cash benefit for any CO₂ concentration. The cost of maintaining a concentration can be obtained from a prediction of the ventilation air exchange rate and the unit price of CO₂. The CO₂ set-point is evaluated as the concentration that maximizes the net profit rate. (C) 1996 Silsoe Research Institute

KEYWORDS: CO₂-ENRICHMENT, CUCUMBER, FRUIT-GROWTH, GREENHOUSES, LYCOPERSICON-ESCULENTUM MILL, MODEL, PLANTS, TEMPERATURE, VENTILATION

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Akimoto, M., A. Shirai, K. Ohtaguchi, and K. Koide. 1998. Carbon dioxide fixation and polyunsaturated fatty acid production by the red alga *Porphyridium cruentum*. *Applied Biochemistry and Biotechnology* 73(2-3):269-278.

Focusing on CO₂ fixation, photoautotrophic cultivation of the red alga *Porphyridium cruentum* was investigated by means of a batch culture under a 5% CO₂-enriched atmosphere. The algal growth kinetics was successfully described with a logistic model, and simulation of a continuous culture under the optimum growth conditions (30 degrees C, 12 klux and 1.18 g-cells/L) showed that the algal CO₂-fixation activity could reach 0.66 g-CO₂/(L X d). Under the same growth conditions, eicosapentaenoic acid (20:5 n-3, EPA) and arachidonic acid (20:4 n-6, ARA) yields were similarly calculated to be 3.6 mg-EPA/(L X d) and 6.5 mg-ARA/(L X d), respectively.

KEYWORDS: CULTIVATION, GROWTH, LIGHT-INTENSITY, TEMPERATURE

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Akin, D.E., B.A. Kimball, J.R. Mauney, R.L. Lamorte, G.R. Hendrey, K. Lewin, J. Nagy, and R.N. Gates. 1994. Influence of enhanced CO₂ concentration and irrigation on sudangrass digestibility. *Agricultural and Forest Meteorology* 70(1-4):279-287.

An experimental line of sudangrass (*Sorghum bicolor* L. Moench) was included in the free-air CO₂ enrichment (FACE) project in 1991 at the University of Arizona Maricopa Agricultural Center to evaluate the effect of ambient (approximately 370 mumol mol⁻¹) and enriched (550 mumol mol⁻¹) CO₂ in well-watered or water-stressed plots. Our specific objective was to determine modifications caused by these environmental effects on the percentages of morphological parts and the fiber components, and on the in vitro digestibility in vegetative and mature harvests. Enrichment with CO₂ did not (P > 0.05) change the percentages of morphological parts or fiber components, or the digestibility of any of the morphological components. Protein levels tended to be lower in CO₂-enriched plants. However, water-stressed plants tended to have a higher proportion of leaves (blades and sheaths) and a lower proportion of stems, were more digestible, and had lower amounts of anti-quality, aromatic compounds within the plant cell. Stems had the highest digestibility of all morphological components (about 75% in vegetative plants) despite the lowest levels of protein. Stems also showed the greatest changes caused by all treatments, including a 20% decline in digestibility from vegetative to mature samples. The results indicate that enriching CO₂ to 550 mumol mol⁻¹ did not reduce digestibility of sudangrass.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT

22

Akin, D.E., B.A. Kimball, W.R. Windham, P.J. Pinter, G.W. Wall, R.L. Garcia, R.L. Lamorte, and W.H. Morrison. 1995. Effect of free-air CO₂ enrichment (FACE) on forage quality of wheat. *Animal Feed Science and Technology* 53(1):29-43.

Wheat (*Triticum aestivum* L., cultivar 'Yecora rojo') was grown in ambient (370 $\mu\text{mol mol}^{-1}$) or enriched (550 $\mu\text{mol mol}^{-1}$) concentrations of CO₂ in the free-air CO₂ enrichment (FACE) project, and components were analyzed for in vitro digestibility, fiber constituents, and crude protein. Four replicated plots of each CO₂ treatment were split for irrigation: 'wet' regions received 60 cm of water and 'dry' regions received 30 cm of water through underground tubes. Enriched CO₂ concentrations had no effect on in vitro digestion of intact sections of young (26-32-day-old plants) leaf blades except at 24-27 h incubation, at which time enriched leaves were lower in digestibility than control ones. Enriched CO₂ concentrations increased the content of acid detergent fiber (ADF) and cellulose of young wet leaves. Sections of main shoots at 26 days tended to have increased digestibility with elevated CO₂ levels. Enriched CO₂ concentrations did not alter the digestibility of flag leaves from 105-day-old plants or of flag leaves, uppermost stems, and sheaths from plants at full grain maturity. Enriched CO₂ levels reduced the acid detergent lignin (ADL) and tended to reduce the protein of leaves from 105-day-old plants. For mature leaf blades, neutral detergent fiber, ADF, and cellulose were, or tended to be, higher while protein content tended to be lower in elevated CO₂-grown plants; for both CO₂ treatments, 'dry' leaves were higher in digestibility and lower in ADL than 'wet' samples. Mature stems plus sheaths had lower protein contents in plants grown in elevated CO₂. Results indicated that enriched CO₂ concentrations to 550 $\mu\text{mol mol}^{-1}$ did not substantially alter wheat in vitro digestibility, regardless of irrigation treatment. Elevated CO₂ altered fiber components and protein, but these were not consistent among parts and harvests.

KEYWORDS: CELL-WALLS, ECOSYSTEMS, MICROSPECTROPHOTOMETRY, PHENOLIC CONSTITUENTS

23

Akin, D.E., L.L. Rigsby, G.R. Gamble, W.H. Morrison, B.A. Kimball, P.J. Pinter, G.W. Wall, R.L. Garcia, and R.L. Lamorte. 1995. Biodegradation of plant-cell walls, wall carbohydrates, and wall aromatics in wheat grown in ambient or enriched CO₂ concentrations. *Journal of the Science of Food and Agriculture* 67(3):399-406.

Mature internodes from wheat (*Triticum aestivum* L.) grown in control (ambient at c 370 $\mu\text{mol mol}^{-1}$) or enriched (to 550 $\mu\text{mol mol}^{-1}$) concentrations of atmospheric CO₂ in the free-air CO₂ enrichment (FACE) system were analyzed for potential changes in biodegradation of constituents due to predicted increases in atmospheric levels of CO₂. The first internodes below the grain were incubated with the lignocellulose-degrading white rot fungus, *Phanerochaete chrysosporium* K-3, or incubated without microorganisms. Plant samples were then analyzed for dry weight loss, disposition of specific cell types to biodegradation using electron microscopy, carbohydrates and lignin using solid state NMR spectroscopy, and ester- and ether-linked aromatics using gas chromatography. *Phanerochaete chrysosporium* extensively degraded stems cells (c 75%) and both carbohydrate and aromatic portions of the wheat stems proportionately more carbohydrates were removed by the fungus from the stems. Enriched CO₂ did not affect the chemical composition of wheat stems or the biodegradation by *P. chrysosporium* of plant cell walls or wall components for the most part. Data from various methods all indicated that enriched CO₂ did not substantially alter the biodegradation of wheat cell wall internodes or wall components. Evidence was not found for an influence on C cycling

due to CO₂ concentrations in this study.

KEYWORDS: ECOSYSTEMS, LIGNINS, PHENOLIC CONSTITUENTS

24

Alagusundaram, K., D.S. Jayas, N.D.G. White, W.E. Muir, and R.N. Sinha. 1995. Controlling *Cryptolestes ferrugineus* (Stephens) adults in wheat stored in bolted-metal bins using elevated carbon-dioxide. *Canadian Agricultural Engineering* 37(3):217-223.

Experiments were conducted in two 5.56 m-diameter farm bins to determine the mortality of caged adult rusty grain beetles, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: cucujidae), under elevated carbon dioxide (CO₂) concentrations. The bins were filled with wheat to a depth of 2.5 m. Dry ice was used to create high CO₂ concentrations in the wheat bulks. Two different modes of application of dry ice were used: (i) pellets on the grain surface and in the aeration duct and (ii) pellets on the grain surface and blocks in insulated boxes on the grain surface. The pellets exposed to the ambient conditions on the grain surface and in the aeration duct sublimated quickly and had to be replenished at frequent intervals. Dry ice blocks in insulated boxes, however, maintained high CO₂ concentrations without replenishment for over 15 d. In both modes of application, the observed CO₂ concentrations in the intergranular gas were about 15% and 30% (all the CO₂ concentrations given in this article are on a volume basis) at 2.05 m and 0.55 m above the floor, respectively. At 0.55 m above the floor, the mortality of rusty grain beetle adults was more than 90% while in the top portions of the bulk (2.05 m above the floor) the mortality was only 30%. On an average about two thirds of the insects were killed. The use of controlled atmosphere treatment within an integrated pest management context is outlined.

KEYWORDS: INSECTS

25

Alberto, A.M.P., L.H. Ziska, C.R. Cervancia, and P.A. Manalo. 1996. The influence of increasing carbon dioxide and temperature on competitive interactions between a C₃ crop, rice (*Oryza sativa*) and a C-4 weed (*Echinochloa glabrescens*). *Australian Journal of Plant Physiology* 23(6):795-802.

Many of the most troublesome weeds in agricultural systems are C-4 plants. As atmospheric CO₂ increases it is conceivable that competitive ability of these weeds could be reduced relative to C-3 crops such as rice. At the International Rice Research Institute (IRRI) in the Philippines, rice (IR72) and one of its associated C-4 weeds, *Echinochloa glabrescens*, were grown from seeding to maturity using replacement series mixtures (100:0, 75:25, 50:50, 25:75, and 0:100, % rice:% weed) at two different CO₂ concentrations (393 and 594 $\mu\text{mol mol}^{-1}$) in naturally sunlit glasshouses. Since increasing CO₂ may also result in elevated growth temperatures, the response of rice to each CO₂ concentration was also examined at day/night temperatures of 27/21 and 37/29 degrees C. At 27/21 degrees C, increasing the CO₂ concentration resulted in a significant increase in above ground biomass (+47%) and seed yield (+55%) of rice when averaged over all mixtures. For *E. glabrescens*, the C-4 species, no significant effect of CO₂ concentration on biomass or yield was observed. When grown in mixture, the proportion of rice biomass increased significantly relative to that of the C-4 weed at all mixtures at elevated CO₂. Evaluation of changes in competitiveness (by calculation of plant relative yield (PRY) and replacement series diagrams) of the two species demonstrated that, at elevated CO₂, the competitiveness of rice was increased relative to that of *E. glabrescens*. However, at the higher growth temperature (37/29 degrees C), growth and reproductive stimulation of rice by elevated CO₂ was reduced compared to the lower growth temperature. This resulted in a reduction in the proportion of rice:weed biomass present in all

mixtures relative to 27/21 degrees C and a greater reduction in PRY in rice relative to *E. glabrescens*. Data from this experiment suggest that competitiveness could be enhanced in a C-3 crop (rice) relative to a C-4 weed (*E. glabrescens*) with elevated CO₂ alone, but that simultaneous increases in CO₂ and temperature could still favour a C-4 species.

KEYWORDS: DRY-MATTER, ENRICHMENT, GROWTH, NITROGEN, PLANTS, WHEAT

26

Alcamo, J., G.J.J. Kreileman, M.S. Krol, and G. Zuidema. 1994. Modeling the global society-biosphere-climate system .1. Model description and testing. *Water, Air, and Soil Pollution* 76(1-2):1-35.

This paper describes the IMAGE 2.0 model, a multi-disciplinary, integrated model designed to simulate the dynamics of the global society-biosphere-climate system. The objectives of the model are to investigate linkages and feedbacks in the system, and to evaluate consequences of climate policies. Dynamic calculations are performed to year 2100, with a spatial scale ranging from grid (0.5-degrees x 0.5-degrees latitude- longitude) to world regional level, depending on the sub-model. The model consists of three fully linked sub-systems: Energy- Industry, Terrestrial Environment, and Atmosphere-Ocean. The Energy-Industry models compute the emissions of greenhouse gases in 13 world regions as a function of energy consumption and industrial production. End use energy consumption is computed from various economic/demographic driving forces. The Terrestrial Environment models simulate the changes in global land cover on a grid-scale based on climatic and economic factors, and the flux of CO₂ and other greenhouse gases from the biosphere to the atmosphere. The Atmosphere-Ocean models compute the buildup of greenhouse gases in the atmosphere and the resulting zonal-average temperature and precipitation patterns. The fully linked model has been tested against data from 1970 to 1990, and after calibration can reproduce the following observed trends: regional energy consumption and energy-related emissions, terrestrial flux of CO₂ and emissions of greenhouse gases, concentrations of greenhouse gases in the atmosphere, and transformation of land cover. The model can also simulate long term zonal average surface and vertical temperatures.

KEYWORDS: CARBON-CYCLE, CO₂, SENSITIVITY

27

Alcamo, J., G.J. Vandenborn, A.F. Bouwman, B.J. Dehaan, K.K. Goldewijk, O. Klepper, J. Krabec, R. Leemans, J.G.J. Olivier, A.M.C. Toet, H.J.M. Devries, and H.J. Vanderwoerd. 1994. Modeling the global society-biosphere-climate system .2. Computed scenarios. *Water, Air, and Soil Pollution* 76(1-2):37-78.

This paper presents scenarios computed with IMAGE 2.0, an integrated model of the global environment and climate change. Results are presented for selected aspects of the society- biosphere-climate system including primary energy consumption, emissions of various greenhouse gases, atmospheric concentrations of gases, temperature, precipitation, land cover and other indicators. Included are a "Conventional Wisdom" scenario, and three variations of this scenario: (i) the Conventional Wisdom scenario is a reference case which is partly based on the input assumptions of the IPCC's IS92a scenario; (ii) the "Biofuel Crops" scenario assumes that most biofuels will be derived from new cropland; (iii) the "No Biofuels" scenario examines the sensitivity of the system to the use of biofuels; and (iv) the "Ocean Realignment" scenario investigates the effect of a large-scale change in ocean circulation on the biosphere and climate. Results of the biofuel scenarios illustrate the importance of examining the impact of biofuels on the full range of greenhouse gases, rather than only CO₂. These scenarios also indicate possible side effects of the land requirements for energy crops. The

Ocean Realignment scenario shows that an unexpected, low probability event can both enhance the build-up of greenhouse gases, and at the same time cause a temporary cooling of surface air temperatures in the Northern Hemisphere. However, warming of the atmosphere is only delayed, not avoided.

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Allen, D.J., I.F. McKee, P.K. Farage, and N.R. Baker. 1997. Analysis of limitations to CO₂ assimilation on exposure of leaves of two *Brassica napus* cultivars to UV-B. *Plant, Cell and Environment* 20(5):633-640.

Apex and Bristol cultivars of oilseed rape (*Brassica napus*) were irradiated with 0.63 W m⁻² of UV-B over 5 d. Analyses of the response of net leaf carbon assimilation to intercellular CO₂ concentration were used to examine the potential limitations imposed by stomata, carboxylation velocity and capacity for regeneration of ribulose 1,5-bisphosphate on leaf photosynthesis. Simultaneous measurements of chlorophyll fluorescence were used to estimate the maximum quantum efficiency of photosystem II (PSII) photochemistry, the quantum efficiency of linear electron transport at steady-state photosynthesis, and the light and CO₂-saturated rate of linear electron transport. Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) content and activities were assayed in vitro. In both cultivars the UV-B treatment resulted in decreases in the light-saturated rate of CO₂ assimilation, which were accompanied by decreases in carboxylation velocity and Rubisco content and activity. No major effects of UV-B were observed on end-product inhibition and stomatal limitation of photosynthesis or the rate of photorespiration relative to CO₂ assimilation. In the Bristol cultivar, photoinhibition of PSII and loss of linear electron transport activity were observed when CO₂ assimilation was severely inhibited. However, the Apex cultivar exhibited no major inhibition of PSII photochemistry or linear electron transport as the rate of CO₂ assimilation decreased. It is concluded that loss of Rubisco is a primary factor in UV-B inhibition of CO₂ assimilation.

KEYWORDS: ENHANCED RADIATION, HIGHER-PLANTS, ORYZA-SATIVA, PHOTOSYNTHETIC ELECTRON-TRANSPORT, PHOTOSYSTEM, PISUM-SATIVUM, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, ULTRAVIOLET-RADIATION, VIGNA-SINENSIS L

29

Allen, L.H. 1992. Free-air CO₂ enrichment field experiments - an historical overview. *Critical Reviews in Plant Sciences* 11(2-3):121-134.

KEYWORDS: CARBON DIOXIDE, CO₂, COTTON, CROPS, FUMIGATION, GROWN SOYBEANS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SULFUR-DIOXIDE, SYSTEM

30

Allen, L.H., E.C. Bisbal, and K.J. Boote. 1998. Nonstructural carbohydrates of soybean plants grown in subambient and superambient levels of CO₂. *Photosynthesis Research* 56(2):143-155.

Elevated carbon dioxide (CO₂) concentration increases plant photosynthesis, biomass and carbohydrate accumulation. Since plants have grown in low CO₂ (200 to 300 μmol mol⁻¹) for the last several million years, how will they use extra photoassimilate as the atmospheric CO₂ continues to rise? The objectives were to determine the effects of past, present and projected future levels of CO₂ on diurnal and seasonal patterns of total nonstructural carbohydrate (TNC) concentration of soybean [*Glycine max* (L.) Merr.] tissues. Plants were grown at 160, 220, 280, 330, 660 and 990 μmol mol⁻¹ CO₂ in outdoor, sunlit chambers wherein CO₂ uptake rates were measured continuously. Early morning and late afternoon plant samples were taken at eight dates. The

TNC concentration of leaves, petioles and stems increased as CO₂ increased. Canopy photosynthetic rates also increased with increasing CO₂, apparently without any negative impact of increased leaf TNC. Concentrations of TNC in all vegetative tissues were lower in the morning than the afternoon, which indicates overnight mobilization and utilization of carbohydrates for growth processes. The concentration of TNC was lowest in all plant components during rapid vegetative growth at Vg to R2 developmental stages. Leaves of all plants, especially those grown in superambient CO₂, contained large pools of TNC at plant maturity, which indicated that not all of the reserves were utilized for seed yield. Soybean cultivars for the future should be designed to utilize carbohydrates more readily for seed production so that greater benefit can be realized from rising atmospheric CO₂.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, EXPORT, LMERR PLANTS, LEAF, LEAVES, LIGHT, PHOTOSYNTHETIC RESPONSE, REPRODUCTIVE GROWTH, STARCH CONCENTRATION, TEMPERATURE

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Allen, L.H., E.C. Bisbal, K.J. Boote, and P.H. Jones. 1991. Soybean dry-matter allocation under subambient and superambient levels of carbon-dioxide. *Agronomy Journal* 83(5):875-883.

Rising atmospheric carbon dioxide concentration [CO₂] is expected to cause increases in crop growth and yield. The objective of this study was to investigate effects of subambient, as well as superambient, [CO₂] on soybean [*Glycine max* (L.) Merr.] dry matter production and allocation for two reasons: to assess response of plants to prehistoric as well as future expected CO₂ levels and to increase confidence in [CO₂] response curves by imposing a wide range of [CO₂] treatments. Soybean was grown in outdoor, sunlit, controlled- environment chambers at CO₂ levels of 160, 220, 280, 330, 660, and 990- μ -mol (CO₂) mol⁻¹ (air). Total dry matter growth rates during the linear phase of vegetative growth were 5.0, 8.4, 10.9, 12.5, 18.2, and 20.7 g m⁻² d⁻¹ for the above respective [CO₂]. Samples taken from 24 to 94 d after planting showed that the percentage of total plant mass in leaf trifoliolates decreased with increasing [CO₂] whereas the percentage in structural components (petioles and stems) increased. At final harvest the respective [CO₂] treatments resulted in 38, 53, 62, 100, 120, and 92% seed yield with respect to the 330- μ -mol mol⁻¹ treatment. Total dry weight responses were similar. Late season spider mite damage of the 990 and 280- μ -mol mol⁻¹ treatments reduced yields. These data confirm not only that rising CO₂ should increase plant growth, but also that plant growth was probably seriously limited by atmospheric [CO₂] in preindustrial revolution times back to the previous global glaciation.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, CHAMBERS, DEVELOPMENTAL STAGES, PHOTOSYNTHESIS, PLANT GROWTH, TRANSPIRATION RESPONSES, WATER-USE, WEIGHT, YIELD

32

Allen, L.H., B.G. Drake, H.H. Rogers, and J.H. Shinn. 1992. Field techniques for exposure of plants and ecosystems to elevated CO₂ and other trace gases. *Critical Reviews in Plant Sciences* 11(2-3):85-119.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, CARBON-DIOXIDE CONCENTRATIONS, ESTUARINE MARSH, OPEN-AIR FUMIGATION, OPEN-TOP CHAMBERS, PORTABLE CHAMBER, SOYBEAN CANOPIES, TRANSPIRATION RESPONSES, VENTILATED CHAMBER, WATER-VAPOR EXCHANGE

33

Allen, L.H., R.R. Valle, J.W. Jones, and P.H. Jones. 1998. Soybean leaf water potential responses to carbon dioxide and drought. *Agronomy*

Journal 90(3):375-383.

Rising CO₂ can have direct effects on crop water relations and indirect effects on water available for growth. We studied the effects of elevated CO₂ and drought on leaf water relations of soybean [*Glycine max* (L.) Merr. cv. Bragg] and considered the hypothesis of osmotic adjustment mediated by increased photosynthesis (Hypothesis 1) vs. the hypothesis of water conservation mediated by decreased stomatal conductance (Hypothesis 2) to explain improved water relations of plants growing under elevated CO₂. In Exp. 1, soybean was grown at 330, 450, 660, and 800 μ mol mol⁻¹ CO₂ in sunlit, closed- circulation, controlled- environment chambers under well-watered conditions. Leaf total water potential (WP), osmotic potential (OP), and turgor potential (TP) were measured at midday during V4 to R6 stages of development. In Exp. 2 (well-watered, R1-R3) and Exp. 3 (13-d drying cycle, R6 seed filling), soybean was grown at 330 and 660 μ mol mol⁻¹ CO₂ and WP, OP, and TP were measured five times per day on sunlit and shaded leaves. In Exp. 3, stomatal conductance (g(s)) and transpiration rate (TR) of leaves were also measured. Experiments 1 and 2 showed that elevated CO₂ increased TP and decreased OP, but did not affect leaf WP, thus favoring Hypothesis 1. In Exp. 3, leaf WP was higher in elevated than ambient CO₂. Diurnal TP was higher in elevated than ambient CO₂ at the beginning of drought, and was maintained longer each day as drought progressed. At the end of drought, TP and WP was higher in elevated than ambient CO₂. Elevated CO₂ leaves had lower TR because of lower g(s) than ambient CO₂ counterparts. Thus, Exp. 3 supported Hypothesis 2, that both stressed and nonstressed plants in elevated CO₂ have a better water status (e.g., higher TP) than plants in ambient CO₂ due to water conservation mediated by decreased g(s). Remobilization of leaf nutrients during seed filling may limit the capability for osmotic adjustment. Regardless of the mechanisms, growth of plants in elevated CO₂ should be less affected by drought than plants in ambient CO₂.

KEYWORDS: DIFFERENT CO₂ ENVIRONMENTS, FIELD, LEAVES, MAIZE, NITROGEN, OSMOTIC ADJUSTMENT, PLANT GROWTH, STRESS, USE EFFICIENCY, YIELD

34

Allen, L.H., R.R. Valle, J.W. Mishoe, and J.W. Jones. 1994. Soybean leaf gas-exchange responses to carbon-dioxide and water-stress. *Agronomy Journal* 86(4):625-636.

As global carbon dioxide concentrations rise, we need to understand the combination of direct effects of this gas and the anticipated effects of climate change, including drought, on physiology and growth of all crops. Effects Of CO₂ on plants begin at the leaf level; our objectives, therefore, were to determine interrelationships among factors governing gas exchange responses of soybean [*Glycine max* (L.) Merr.] leaves to elevated CO₂ and water stress. Photosynthetic CO₂ assimilation and transpiration rates were measured in cuvettes on leaflets of soybean (cv. Bragg) grown in controlled- environment chambers at 330 and 660 μ mol CO₂ Mol⁻¹ air. Leaflets at high CO₂, either water-stressed or well-watered, had higher photosynthetic and lower transpiration rates, and therefore higher water-use efficiencies (WUE), than those at Control CO₂ levels. As irrigation was withheld during an 11-d period, WUE decreased about 30 to 50% with respect to the well- watered treatments. Midday leaf temperature and leaf-to-air vapor pressure gradient levels increased as the water stress progressed. For water stress treatments, midday leaf conductance (G(lw)) was generally higher and residual internal conductance (G(r)) was generally lower in low than in high CO₂. Ratios of midday G(r)/G(lc), were nearly constant throughout the period in both the stressed and the well-watered treatments. The ratios of intercellular C(i), to ambient C(a), CO₂ concentration (i.e., C(i)/C(a)) during the water stress period remained similar to the respective nonstressed treatments within each CO₂ level. These findings support the concept that leaf conductances are governed by CO₂ assimilation rates under water-stressed as well as unstressed conditions.

KEYWORDS: *ABSCISIC- ACID, CARBOXYLASE, DIFFERENT CO2 ENVIRONMENTS, FIELD, GROWTH, LEAVES, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TRANSPIRATION RATE, WHEAT*

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Allen, L.H., R.R. Valle, J.W. Mishoe, J.W. Jones, and P.H. Jones. 1990. Soybean leaf gas-exchange responses to CO₂ enrichment. *Soil and Crop Science Society of Florida Proceedings* 49:192-198.

36

Almeida, J.P.F., A. Luscher, M. Frehner, A. Oberson, and J. Nosberger. 1999. Partitioning of P and the activity of root acid phosphatase in white clover (*Trifolium repens* L.) are modified by increased atmospheric CO₂ and P fertilisation. *Plant and Soil* 210(2):159-166.

The growth response of white clover (*Trifolium repens* L.) to the expected increase in atmospheric partial pressure of CO₂ (p(CO₂)) may depend on P availability. A decrease in the rate of transpiration due to increased p(CO₂) may reduce the amount of P transported to the shoot, thereby causing a change in the partitioning of P between the root and shoot. To test these hypotheses, four concentrations of P in the nutrient solution, combined with two p(CO₂) treatments, were applied to nodulated white clover plants. Compared to ambient p(CO₂) (35 Pa), twice ambient p(CO₂) (70 Pa) reduced the rate of transpiration but did not impair the total P uptake per plant. However, at twice ambient p(CO₂) and a moderate to high supply of P, concentrations of structural P and soluble P (Pi) were lower in the leaves and higher in the roots. The activity of root acid phosphatase was lower at twice ambient p(CO₂) than at ambient p(CO₂); it depended on the Pi concentration in the roots. At the highest P concentration, twice ambient p(CO₂) stimulated photosynthesis and the growth rate of the plant without affecting the concentration of nonstructural carbohydrates in the leaves. However, at the lower P concentrations, plants at twice ambient p(CO₂) lost their stimulation of photosynthesis in the afternoon, they accumulated nonstructural carbohydrates in the leaves and their growth rate was not stimulated; indicating C-sink limitation of growth. P nutrition will be crucial to the growth of white clover under the expected future conditions of increased p(CO₂).

KEYWORDS: *AIR, BEAN-PLANTS, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, MAGNESIUM-DEFICIENCY, PHOSPHORUS, SOURCE-SINK RELATIONS, SUBTERRANEUM L*

37

Alvarez, R., M. Alconada, and R. Lavado. 1999. Sewage sludge effects on carbon dioxide-carbon production from a desurfaced soil. *Communications in Soil Science and Plant Analysis* 30(13-14):1861-1866.

Desurfaced soils are found near cities in the Pampean Region of Argentina because A horizons were used for brick production. These soils are not suitable for agriculture. Application of sewage sludge is a tool for improving soil productivity, but its effects on the environment are not thoroughly understood. Production of carbon dioxide (CO₂)-carbon (C) in the field from a desurfaced soil in which 25 Mg dry matter ha⁻¹ of sewage sludge were applied the first year and 10 Mg dry matter ha⁻¹, the second year was evaluated during a corn (*Zea mays* L.) growing cycle. Microbial biomass and metabolic activity were also measured. Sludge applications produced an increase of the CO₂-C efflux in the field of 30-50% during summer. Microbial biomass was not affected by sludge some months after the application, but metabolic activity and organic matter mineralization were enhanced. The increase of the CO₂-C emission from the soil represented 21% of the sludge C

applied the year of the experiment and 15% of the C applied the year before. Consequently, an important quantity of the sludge C was retained in the soil.

KEYWORDS: *CROPS, GLUCOSE, HEAVY-METALS, MAIZE, MANURE, MICROBIAL BIOMASS DYNAMICS, RESIDUE*

38

Ambus, P., and G.P. Robertson. 1999. Fluxes of CH₄ and N₂O in aspen stands grown under ambient and twice-ambient CO₂. *Plant and Soil* 209(1):1-8.

Elevated atmospheric CO₂ has the potential to change below-ground nutrient cycling and thereby alter the soil-atmosphere exchange of biogenic trace gases. We measured fluxes of CH₄ and N₂O in trembling aspen (*Populus tremuloides* Michx.) stands grown in open-top chambers under ambient and twice-ambient CO₂ concentrations crossed with 'high' and low soil-N conditions. Flux measurements with small static chambers indicated net CH₄ oxidation in the open-top chambers. Across dates, CH₄ oxidation activity was significantly (P < 0.05) greater with ambient CO₂ (8.7 μg CH₄-C m⁻² h⁻¹) than with elevated CO₂ (6.5 μg CH₄-C m⁻² h⁻¹) in the low N soil. Likewise, across dates and soil N treatments CH₄ was oxidized more rapidly (P < 0.05) in chambers with ambient CO₂ (9.5 μg CH₄-C m⁻² h⁻¹) than in chambers with elevated CO₂ (8.8 μg CH₄-C m⁻² h⁻¹). Methane oxidation in soils incubated in serum bottles did not show any response to the CO₂ treatment. We suggest that the depressed CH₄ oxidation under elevated CO₂ in the field chambers is due to soil moisture which tended to be higher in the twice-ambient CO₂ treatment than in the ambient CO₂ treatment. Phase I denitrification (denitrification enzyme activity) was 12-26% greater under elevated CO₂ than under ambient CO₂ in the 'high' N soil; one sampling, however, showed a 39% lower enzyme activity with elevated CO₂. In both soil N treatments, denitrification potentials measured after 24 or 48 h were between 11% and 21% greater (P < 0.05) with twice-ambient CO₂ than with ambient CO₂. Fluxes of N₂O in the open-top chambers and in separate 44 cm(2) cores +/-N fertilization were not affected by CO₂ treatment and soil N status. Our data show that elevated atmospheric CO₂ may have a negative effect on terrestrial CH₄ oxidation. The data also indicated temporary greater denitrification with elevated CO₂ than with ambient CO₂. In contrast, we found no evidence for altered fluxes of N₂O in response to increases in atmospheric CO₂.

KEYWORDS: *ATMOSPHERIC METHANE CONSUMPTION, DENITRIFICATION, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GAS FLUXES, GRASSLAND, NITROUS-OXIDE, RESPONSES, TALLGRASS PRAIRIE, TEMPERATE FOREST SOILS*

39

Amiro, B.D., J.I. MacPherson, and R.L. Desjardins. 1999. BOREAS flight measurements of forest-fire effects on carbon dioxide and energy fluxes. *Agricultural and Forest Meteorology* 96(4):199-208.

Fire is the dominant stand-replacing agent in the Canadian boreal forest, but few quantitative measurements are available on the micrometeorological effects of fire. Airborne flux measurements during the BOREAS experiment were referenced to age of burn along a 500-km transect through Saskatchewan and Manitoba, Canada. These data for 1-, 5-, and 7-year-old burns were supplemented with 15- and 30-year-old-burn data from the BOREAS northern study site near Thompson, Manitoba. Data were available near midday only and included the June, July and September campaigns during 1994, and July of 1996. Surface radiometric temperature increased by up to 6 degrees C and remained elevated even 15 years after fire. Net radiation was largely unaffected whereas albedo decreased in the first year post-fire but recovered by the fifth year. Sensible heat flux increased by 10-20% for the first few years

after the fire and then decreased. Latent heat flux slightly decreased after the fire, causing the Bowen ratio to increase by ca. 50% for 7 years post-fire. The CO₂ flux was reduced for the 15-year period after fire with the greatest reduction to ca. 25% of control areas during the year following fire. However, diurnal and annual data are needed to determine the total impact of fire on the boreal-forest carbon balance. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ASPEN FOREST, ATMOSPHERE, ECOSYSTEMS, EXCHANGES, MICROBIAL BIOMASS, NORTHERN, PINE FOREST, SOIL RESPIRATION, WATER-VAPOR, WILDFIRE

40

Amoroso, G., C. Weber, D. Sultemeyer, and H. Fock. 1996. Intracellular carbonic anhydrase activities in *Dunaliella tertiolecta* (Butcher) and *Chlamydomonas reinhardtii* (Dangeard) in relation to inorganic carbon concentration during growth: Further evidence for the existence of two distinct carbonic anhydrases associated with the chloroplasts. *Planta* 199(2):177-184.

Using mass-spectrometric measurements of O-18 exchange from (CO₂)-C-13-O-18 intracellular carbonic anhydrase (CA) activity was investigated in the unicellular green algae *Dunaliella tertiolecta* and *Chlamydomonas reinhardtii* which were either grown on air enriched with 5% CO₂ (high-C-i cells) or on air (low-C-i cells). In *D. tertiolecta* high- and low-C-i cells had detectable levels of internal CA activity when measured under in-vivo conditions and this activity could be split up into three distinct forms. One CA was not associated with the chloroplasts, while two isozymes were found to be located within the plastids. The activities of all intracellular CAs were always about twofold higher in low than in high -C-i cells of *D. tertiolecta* and the chloroplastic enzymes were completely induced within 4 h of adaptation to air. One of the chloroplastic CAs was found to be soluble the other was insoluble. In addition to the physical differences, MgSO₄ in vitro caused a more than twofold stimulation of the soluble activity while the insoluble form of CA remained rather unaffected. In *C. reinhardtii*, MgSO₄ increased the soluble CA activity by 346% and the concentration of MgSO₄ required for half-maximum stimulation was between 10 and 15 mM. Again, the insoluble CA activity was not affected by MgSO₄. Furthermore, the soluble isoenzyme was considerably more sensitive to ethoxzolamide, a potent inhibitor of CA, than the insoluble enzyme. The concentration of inhibitor causing 50% inhibition of soluble CA activity was 110 and 85 μM ethoxzolamide for *D. tertiolecta* and *C. reinhardtii*, respectively. From these data we conclude that the two chloroplast-associated CAs are distinct enzymes.

KEYWORDS: CELL-SURFACE, CO₂, CYANOBACTERIUM SYNECHOCOCCUS PCC7942, INCREASES, INTACT CHLOROPLASTS, MICROALGAE, O-18 EXCHANGE, PHOTOSYNTHESIS, SALINA, TRANSPORT

41

Amthor, J.S. 1991. Respiration in a future, higher-CO₂ world. *Plant, Cell and Environment* 14(1):13-20.

Apart from its impact on global warming, the annually increasing atmospheric [CO₂] is of interest to plant scientists primarily because of its direct influence on photosynthesis and photorespiration in C₃ species. But in addition, 'dark' respiration, another major component of the carbon budget of higher plants, may be affected by a change in [CO₂] independent of an increase in temperature. Literature pertaining to an impact of [CO₂] on respiration rate is reviewed. With an increase in [CO₂], respiration rate is increased in some cases, but decreased in others. The effects of [CO₂] on respiration rate may be direct or indirect. Mechanisms responsible for various observations are proposed. These proposed mechanisms relate to changes in: (1) levels of nonstructural

carbohydrates, (2) growth rate and structural phytomass accumulation, (3) composition of phytomass, (4) direct chemical interactions between CO₂ and respiratory enzymes, (5) direct chemical interactions between CO₂ and other cellular components, (6) dark CO₂ fixation rate, and (7) ethylene biosynthesis rate. Because a range of (possibly interactive) effects exist, and present knowledge is limited, the impact of future [CO₂] on respiration rate cannot be predicted. Theoretical considerations and types of experiments that can lead to an increase in the understanding of this issue are outlined.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, DARK RESPIRATION, ENERGY OVERFLOW, GAS-EXCHANGE, GROWTH, LEAF, PHOTOSYNTHESIS, PLANTS, TEMPERATURE

42

Amthor, J.S. 1994. Scaling CO₂-photosynthesis relationships from the leaf to the canopy. *Photosynthesis Research* 39(3):321-350.

Responses of individual leaves to short-term changes in CO₂ partial pressure have been relatively well studied. Whole-plant and plant community responses to elevated CO₂ are less well understood and scaling up from leaves to canopies will be complicated if feedbacks at the small scale differ from feedbacks at the large scale. Mathematical models of leaf, canopy, and ecosystem processes are important tools in the study of effects on plants and ecosystems of global environmental change, and in particular increasing atmospheric CO₂, and might be used to scale from leaves to canopies. Models are also important in assessing effects of the biosphere on the atmosphere. Presently, multilayer and big leaf models of canopy photosynthesis and energy exchange exist. Big leaf models - which are advocated here as being applicable to the evaluation of impacts of 'global change' on the biosphere - simplify much of the underlying leaf-level physics, physiology, and biochemistry, yet can retain the important features of plant-environment interactions with respect to leaf CO₂ exchange processes and are able to make useful, quantitative predictions of canopy and community responses to environmental change. The basis of some big leaf models of photosynthesis, including a new model described herein, is that photosynthetic capacity and activity are scaled vertically within a canopy (by plants themselves) to match approximately the vertical profile of PPFD. The new big leaf model combines physically based models of leaf and canopy level transport processes with a biochemically based model of CO₂ assimilation. Predictions made by the model are consistent with canopy CO₂ exchange measurements, although a need exists for further testing of this and other canopy physiology models with independent measurements of canopy mass and energy exchange at the time scale of 1 h or less.

KEYWORDS: C-3 PLANTS, CARBON DIOXIDE, DARK RESPIRATION, LIGHT-INTENSITY, PHOTOSYNTHETIC CO₂ FIXATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SOURCE-SINK RELATIONS, STOMATAL CONDUCTANCE, SUNFLOWER LEAVES, WATER-USE EFFICIENCY

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Amthor, J.S. 1995. Predicting effects of atmospheric CO₂ partial pressure on forest photosynthesis. *Journal of Biogeography* 22(2-3):269-280.

A mechanistic (i.e. hierarchic or explanatory) model of forest canopy mass and energy exchange that has been previously tested with eddy-correlation measurements in the field - albeit only at present ambient CO₂ partial pressure - was used to predict photosynthetic response of a deciduous *Quercus-Acer* forest in eastern North America to atmospheric CO₂ partial pressure. Four partial pressures of CO₂ were used in simulations: 28 (pre-industrial), 36 (present), 54 and 72 Pa. This is (one of) the first set(s) of predictions of forest photosynthetic response to

CO₂ partial pressure made by a mechanistic forest physiology model shown to accurately predict independent field measurements of whole-forest CO₂ exchange at the hourly time scale. The model includes a biochemically based Farquhar-type model of leaf mesophyll CO₂ assimilation, which is central to its ability to predict photosynthetic response to different CO₂ partial pressures. Whole-forest photosynthesis was positively related to CO₂ partial pressure, as expected. This was the case under both clear and cloudy skies, but the relative response to CO₂ was greater under a clear sky compared to a cloudy sky (the clear sky day was also warmer). Instantaneous water use efficiency (mol CO₂ assimilated per mol H₂O transpired) was positively related to atmospheric CO₂ partial pressure for all conditions included in the simulations. Model predictions indicate that (1) present forest photosynthesis and water use efficiency may be significantly greater than they were in pre-industrial times (per unit ground area of forest) and (2) future higher CO₂ partial pressures could further stimulate forest photosynthesis and water use efficiency, unless future climatic changes have significant negative effects on photosynthesis or acclimation and adaptation processes markedly downregulate photosynthesis in response to greater CO₂ partial pressure.

KEYWORDS: C-3 PLANTS, CANOPY, DECIDUOUS FOREST, ELEVATED CO₂, GAS-EXCHANGE, GROWTH, MODELS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RISING CO₂, SOLAR RADIATION

44

Amthor, J.S. 1995. Terrestrial higher-plant response to increasing atmospheric [CO₂] in relation to the global carbon-cycle. *Global Change Biology* 1(4):243-274.

Terrestrial higher plants exchange large amounts of CO₂ with the atmosphere each year; c. 15% of the atmospheric pool of C is assimilated in terrestrial-plant photosynthesis each year, with an about equal amount returned to the atmosphere as CO₂ in plant respiration and the decomposition of soil organic matter and plant litter. Any global change in plant C metabolism can potentially affect atmospheric CO₂ content during the course of years to decades. In particular, plant responses to the presently increasing atmospheric CO₂ concentration might influence the rate of atmospheric CO₂ increase through various biotic feedbacks. Climatic changes caused by increasing atmospheric CO₂ concentration may modulate plant and ecosystem responses to CO₂ concentration. Climatic changes and increases in pollution associated with increasing atmospheric CO₂ concentration may be as significant to plant and ecosystem C balance as CO₂ concentration itself. Moreover, human activities such as deforestation and livestock grazing can have impacts on the C balance and structure of individual terrestrial ecosystems that far outweigh effects of increasing CO₂ concentration and climatic change. In short-term experiments, which in this case means on the order of 10 years or less, elevated atmospheric CO₂ concentration affects terrestrial higher plants in several ways. Elevated CO₂ can stimulate photosynthesis, but plants may acclimate and (or) adapt to a change in atmospheric CO₂ concentration. Acclimation and adaptation of photosynthesis to increasing CO₂ concentration is unlikely to be complete, however. Plant water-use efficiency is positively related to CO₂ concentration, implying the potential for more plant growth per unit of precipitation or soil moisture with increasing atmospheric CO₂ concentration. Plant respiration may be inhibited by elevated CO₂ concentration, and although a naive C balance perspective would count this as a benefit to a plant, because respiration is essential for plant growth and health, an inhibition of respiration can be detrimental. The net effect on terrestrial plants of elevated atmospheric CO₂ concentration is generally an increase in growth and C accumulation in phytomass. Published estimations, and speculations about, the magnitude of global terrestrial-plant growth responses to increasing atmospheric CO₂ concentration range from negligible to fantastic. Well-reasoned analyses point to moderate global plant responses to CO₂

concentration. Transfer of C from plants to soils is likely to increase with elevated CO₂ concentrations because of greater plant growth, but quantitative effects of those increased inputs to soils on soil C pool sizes are unknown. Whether increases in leaf-level photosynthesis and short-term plant growth stimulations caused by elevated atmospheric CO₂ concentration will have, by themselves, significant long-term (tens to hundreds of years) effects on ecosystem C storage and atmospheric CO₂ concentration is a matter for speculation, not firm conclusion. Long-term field studies of plant responses to elevated atmospheric CO₂ are needed. These will be expensive, difficult, and by definition, results will not be forthcoming for at least decades. Analyses of plants and ecosystems surrounding natural geological CO₂ degassing vents may provide the best surrogates for long-term controlled experiments, and therefore the most relevant information pertaining to long-term terrestrial-plant responses to elevated CO₂ concentration, but pollutants associated with the vents are a concern in some cases, and quantitative knowledge of the history of atmospheric CO₂ concentrations near vents is limited. On the whole, terrestrial higher-plant responses to increasing atmospheric CO₂ concentration probably act as negative feedbacks on atmospheric CO₂ concentration increases, but they cannot by themselves stop the fossil-fuel-oxidation-driven increase in atmospheric CO₂ concentration. And, in the very long-term, atmospheric CO₂ concentration is controlled by atmosphere-ocean C equilibrium rather than by terrestrial plant and ecosystem responses to atmospheric CO₂ concentration.

KEYWORDS: DIOXIDE CONCENTRATION, ELEVATED CO₂, GAS-EXCHANGE, PARTIAL-PRESSURE, PAST 2 CENTURIES, PHOTOSYNTHETIC ACCLIMATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STOMATAL DENSITY, VOSTOK ICE-CORE, WATER-USE EFFICIENCY

45

Amthor, J.S. 1998. Perspective on the relative insignificance of increasing atmospheric CO₂ concentration to crop yield. *Field Crops Research* 58(2):109-127.

Average yield of most crops in many countries increased significantly during the past 50 to 100 years. Although atmospheric CO₂ concentration, [CO₂](a), also increased during that time period, and although crop growth and yield can respond positively to [CO₂](a) increase, yield increases were due mainly to factors other than increasing [CO₂](a). Similarly, some yield increases prior to 1900 were also associated primarily with factors other than changes in [CO₂](a). In particular, past national average yield increases were the result chiefly of technological advances such as nitrogen fertilization; selection of genotypes with increased harvest index and disease resistance; mechanization of planting, cultivation, and harvesting; and chemical weed and pest control. If technology continues to increase average yields at recent rates, near-future increases in [CO₂](a) will have only small impacts on yield in comparison to technology in many countries. Conversely, if future increases in [CO₂](a) are the main drivers of future yield increases, those yield increases will be small. These points are demonstrated through a comparison of (i) long-term records of yield, (ii) data from key controlled-[CO₂] experiments, and (iii) records of past [CO₂](a). Finally, it is noted that continued [CO₂](a) increase may bring with it climatic changes that could have negative or positive impacts on future yield. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: 18TH-CENTURY ENGLAND, AGRICULTURAL PRODUCTIVITY, CARBON DIOXIDE, CLIMATE, ENRICHMENT, PHOTOSYNTHESIS, RESPONSES, SPECULATIONS, TRENDS, WHEAT

46

Amthor, J.S., R.J. Mitchell, G.B. Runion, H.H. Rogers, S.A. Prior, and C.W. Wood. 1994. Energy content, construction cost and

phytomass accumulation of glycine-max (L) merr and sorghum-bicolor (L) moench grown in elevated CO₂ in the field. *New Phytologist* 128(3):443-450.

Grain sorghum [*Sorghum*] bicolor (L.) Moench, a C-4 crop] and soybean [*Glycine max* (L.) Merr. cv. Stonewall, a C-3 crop] plants were grown in ambient (c. 360 µmol(-1)) and twice-ambient (c. 720 µmol(-1)) CO₂ levels in open-top chambers in soil without root constriction. Plant dry mass, energy content, composition and construction cost (i.e. amount of carbohydrate required to synthesize a unit of plant dry mass) were assessed at the end of the growing season. Elevated CO₂ (a) increased phytomass accumulation (kg per plant) in both species, (b) had little effect on energy concentration (MJ kg(-1) plant) but caused large increases in the amount of plant energy per ground area (MJ m(-2) ground), and (c) did not alter specific growth cost (kg carbohydrate kg(-1) plant growth) but greatly increased growth cost per ground area (kg carbohydrate m(-2) ground) because growth was enhanced. For soybean, twice-ambient CO₂ resulted in a 50 % increase in the amount of nitrogen and energy in grain (seed plus pod) per ground area. This response to elevated CO₂ has important implications for agricultural productivity during the next century because the rate of human population growth is exceeding the rate of increase of land used for agriculture so that future food demands can only be met by greater production per ground area.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LEAVES, MAINTENANCE, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPIRATION, RESPONSES, YIELD

47

Andalo, C., B. Godelle, M. Lefranc, M. Mousseau, and I. TillBottraud. 1996. Elevated CO₂ decreases seed germination in *Arabidopsis thaliana*. *Global Change Biology* 2(2):129-135.

The impact of elevated [CO₂] on seed germination was studied in different genotypes of *Arabidopsis thaliana* from natural populations. Two generations of seeds were studied: the maternal generation was produced in the greenhouse (present-day conditions), the offspring generation was produced in two chambers where the CO₂ concentration was either the present atmospheric concentration (about 350 ppm) or elevated (700 ppm). The seeds were tested for proportion of germinated seeds and mean germination time in both chambers to study the impact of elevated [CO₂] during seed production and germination. Elevated [CO₂] during maturation of seeds on the mother-plants decreased the proportion of germinated seeds, while elevated [CO₂] during germination had no effect on the proportion of germinated seeds. However, when seeds were both produced and germinated under elevated [CO₂] (situation expected by the end of next century), germination was slow and low. Moreover, the effect of the [CO₂] treatment differs among genotypes of *Arabidopsis*: there is a strong treatment x genotype interaction. This means that there is ample genetic variance for a selective response modifying the effects of high levels of [CO₂] in natural populations of *Arabidopsis thaliana*. The outcome at the community level will depend on what seeds are available, when they germinate and the resulting competition following germination.

KEYWORDS: GROWTH, PLANTS

48

Andalo, C., C. Raquin, N. Machon, B. Godelle, and M. Mousseau. 1998. Direct and maternal effects of elevated CO₂ on early root growth of germinating *Arabidopsis thaliana* seedlings. *Annals of Botany* 81(3):405-411.

Individuals of *Arabidopsis thaliana*, collected in different natural populations, were grown in controlled and elevated CO₂ in a glasshouse.

Following germination, root growth of progeny of different lines of these populations was studied in control and elevated atmospheric CO₂. No significant direct effect of atmospheric CO₂ concentration could be demonstrated on root growth. An important parental effect was apparent, namely that root length and branching were decreased in seeds collected from a mother plant which had been grown in elevated CO₂. This was correlated with smaller seeds, containing less nitrogen. These parental effects were genetically variable. We conclude that CO₂ may affect plant fitness via parental effects on seed size and early root growth and that the genetic variability shown in our study demonstrates that *Arabidopsis* populations will evolve in the face of this new selective pressure. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELONGATION, ENRICHMENT, PLANT, QUALITY, SEED-GERMINATION, *SENECIO-VULGARIS*, TEMPERATURE, *TRITICUM-AESTIVUM L.*, WHEAT

49

Anderson, J.M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications* 1(3):326-347.

Current models of climate change predict a reduction of area covered by northern coniferous forests and tundra, and an increase in grasslands. These scenarios also indicate a northerly shift in agricultural regions, bringing virgin soils under cultivation. The direct effects of man on tundra, boreal forest, and temperate grassland ecosystems are likely to result in less carbon mobilization from soils and vegetation than from tropical forests. However, as a consequence of climate change, carbon mineralization rates from arctic and sub-arctic soils could be very rapid under warmer and drier conditions because of low stabilization of soil organic matter (SOM) and enhanced microbial responses to small changes in soil moisture and temperature. Predicting the response of these systems to climate change is complicated where the edaphic environment regulating SOM dynamics is not a direct function of macroclimatic conditions. Grasslands contain a greater proportion of highly stabilized SOM than coniferous forests, distributed over greater depth in the soil profile, which is less susceptible to changes in mineralization rates. It is concluded that short-term responses of soil processes to climate change are more predictable in well-drained grassland and forest soils than in waterlogged soils of the tundra and boreal region. Over longer periods of time, however, plant species and soil types will alter in response to new temperature and moisture regimes above- and belowground interacting with the effects of carbon enrichment and changes in nutrient availability. The dynamics of these plant-soil interactions and the future status of soils in different life zones as sources or sinks of carbon is poorly understood. More data are also needed on the distribution of waterlogged forest soils in the boreal zone and responses to warming, which include the production of methane as well as CO₂. The primary recommendation for future research is for integrated studies on plant and soil processes.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DOUGLAS-FIR, LEAF-LITTER DECOMPOSITION, LONG-TERM DECOMPOSITION, NITROGEN-AVAILABILITY, NORTHERN HARDWOODS, SCOTS PINE FOREST, SOIL ORGANIC MATTER, SPRUCE-LICHEN WOODLAND, TEMPERATE ECOSYSTEMS

50

Anderson, P.D., and P.T. Tomlinson. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO₂ and water stress - I. Carbon assimilation and biomass production. *New Phytologist* 140(3):477-491.

The interactive influences of elevated carbon dioxide, water stress, and ontogeny on carbon assimilation and biomass production were

investigated in northern red oak, a species having episodic shoot growth characteristics. Seedlings were grown from acorns through three shoot-growth flushes (8-11 wk) in controlled-environment chambers at 400, 530 or 700 $\mu\text{mol mol}^{-1}$ CO₂ and under well watered or water-stressed soil-moisture regimes. Increasing CO₂ growth concentration from 400 to 700 $\mu\text{mol mol}^{-1}$ resulted in a 34 % increase in net assimilation rate (A), a 31 % decrease in stomatal conductance to water vapour (g(s)) and a 141 % increase in water use efficiency (WUE) in well watered seedlings. In contrast, water-stressed seedlings grown at 700 $\mu\text{mol mol}^{-1}$ CO₂ demonstrated a 69 % increase in A, a 23 % decrease in g(s), and a 104 % increase in WUE. However, physiological responses to increased CO₂ and water stress were strongly modified by ontogeny. During active third-flush shoot growth, A in first-flush and second-flush foliage of water-stressed seedlings increased relative to the quiescent phase following cessation of second-flush growth by an average of 115 %; g(s) increased by an average of 74 %. In contrast, neither A nor g(s) in comparable foliage of well watered seedlings changed in response to active third-flush growth. Whereas seedling growth was continuous through three flushes in well watered seedlings, growth of water-stressed seedlings was minimal following the leaf-expansion stage of the third flush. Through three growth flushes total seedling biomass and biomass allocation to root, shoot and foliage components were very similar in water-stressed seedlings grown at 700 $\mu\text{mol mol}^{-1}$ CO₂ and well watered seedlings grown at 400 $\mu\text{mol mol}^{-1}$ CO₂. Enhancement effects of elevated CO₂ on seedling carbon (C) assimilation and biomass production may offset the negative impact of moderate water stress and are likely to be determined by ontogeny and stress impacts on carbon sink demand.

KEYWORDS: ATMOSPHERIC CO₂, DIOXIDE ENRICHMENT, DROUGHT, GAS-EXCHANGE, GROWTH-RESPONSE, LEAVES, PHOTOSYSTEM, QUERCUS-RUBRA L, RISING CO₂, USE EFFICIENCY

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Andersson, N.E. 1991. The influence of constant and diurnally changing CO₂ concentrations on plant-growth and development. *Journal of Horticultural Science* 66(5):569-574.

Plants of *Ficus benjamina* and miniature rose (*Rosa hybrida* cv. Red Minimo) were grown under four CO₂ treatments. Two had constant CO₂ levels (600 and 900 ppm) and the other two had diurnal changes in CO₂ levels, one increasing from 600 to 1500 ppm and one decreasing from 1500 to 600 ppm, each in four steps of 300 ppm during the day-time. In all treatments 900 ppm CO₂ was maintained during the night when supplementary light was used, except in the treatment with constant 600 ppm where 600 ppm was also continued throughout the night. Plant growth was monitored under both decreasing and increasing natural daylength and irradiance. The tallest plants and greatest increment in height for *Ficus* occurred with plants grown under constant CO₂ concentration at 600 ppm and also with increasing CO₂ concentration. In both experiments the dry weight per pot was lowest when plants were grown under a constant CO₂ concentration at 900 ppm. In both experiments with miniature roses the number of flower buds was significantly increased under diurnally changing CO₂ concentration or when the CO₂ level was constant at 600 ppm compared with a constant 900 ppm. Time to flowering was decreased by constant CO₂ at 900 ppm as compared with the other treatments.

KEYWORDS: ATMOSPHERES, CARBON-DIOXIDE ENRICHMENT, DURATION, EXCHANGE, LIGHT-INTENSITY, ROSE, YIELD

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Andrade, J.L., and P.S. Nobel. 1996. Habitat, CO₂ uptake and growth for the CAM epiphytic cactus *Epiphyllum phyllanthus* in a Panamanian tropical forest. *Journal of Tropical Ecology* 12:291-306.

In the tropical forest of Barro Colorado Island, habitat characteristics, diel acidity changes, CO₂ uptake and growth were investigated for the epiphytic cactus *Epiphyllum phyllanthus* (L.) Haw. It occurred most frequently in tree cavities with its roots in canopy soil and was especially abundant on two tree species: *Platypodium elegans* J. Vogel and *Tabebuia guayacan* (Seem.) Hemsl. Its maximum net CO₂ uptake rates were low under natural conditions (1.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$) but were comparable to those of other CAM and C-3 epiphytes under wet conditions in a screenhouse. Under both natural conditions and in the screenhouse, partial shade enhanced growth and CAM activity. When plants grew under a photosynthetic photon flux of c. 4 $\text{mol m}^{-2} \text{d}^{-1}$, their nocturnal acidity increase and total net CO₂ uptake were twice as much as for plants growing at lower (an average of 2.4 $\text{mol m}^{-2} \text{d}^{-1}$) and higher (7.7 $\text{mol m}^{-2} \text{d}^{-1}$) photosynthetic photon fluxes. Stem elongation was 27% greater at the intermediate photosynthetic photon flux. Seedlings of *E. phyllanthus* survived three months of drought and responded rapidly to rewetting, recovering fully within three days. Transpiration rates and nocturnal acidity increases also recovered to the values of well-watered plants a few days after rewetting, indicating that this species can take advantage of episodic rainfall during the dry season.

KEYWORDS: ACCUMULATION, C-3 BROMELIADS, COMPARATIVE ECOPHYSIOLOGY, CRASSULACEAN ACID METABOLISM, LEAF, OPUNTIA FICUS INDICA, SHADE, VASCULAR EPIPHYTES

53

Andre, M., and H. Ducloux. 1993. Interaction of CO₂ enrichment and water limitations on photosynthesis and water efficiency in wheat. *Plant Physiology and Biochemistry* 31(1):103-112.

Wheat plants (*Triticum aestivum* L. cv. Capitole) were grown in twin closed growth chambers with continuous monitoring of CO₂ and water exchanges. During the vegetative stage the effect of CO₂ enrichment, from 330 to 660 $\mu\text{mol mol}^{-1}$, was studied under irradiance of 660 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with an optimum watering. Comparisons were made with successive experiments in which daily water supply was fixed to a fraction (0.62-0.50-0.25) of the maximal transpiration of previous experiments. In a well-watered canopy, doubling CO₂ decreased transpiration by only 8%. Water use efficiency was increased (factor 1.45) mainly by the stimulation of photosynthesis. Under restricted water supply, photosynthesis of plants was more limited than transpiration. The inhibition of photosynthesis and the increase of water use efficiency can be predicted by a simple diffusion model applied to the response curve of photosynthesis to CO₂, measured on canopy in standard conditions of watering. The main hypothesis is that the equivalent stomatal conductance is reduced proportionally to the water availability, without closure by patching. Under enriched CO₂, the same reduction of leaf surface by water limitation was observed. Photosynthesis was less affected. Therefore, water-use-efficiency was again increased. Doubling CO₂ concentration can compensate for water stress inhibition on CO₂ assimilation. That model also predicts interactions of CO₂ and water stress observed on water-use-efficiency which was increased by a factor up to 5 in comparison with well-watered plants in standard atmosphere. The implications of this study for global change models are discussed.

KEYWORDS: ASSIMILATION, CARBON-DIOXIDE ENRICHMENT, CONDUCTANCE, EXCHANGES, GROWTH, PHASEOLUS-VULGARIS L, PLANTS, SEEDLINGS, STRESS, YIELD

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Andrews, J.A., K.G. Harrison, R. Matamala, and W.H. Schlesinger. 1999. Separation of root respiration from total soil respiration using carbon-13 labeling during Free-Air Carbon Dioxide Enrichment (FACE). *Soil Science Society of America Journal* 63(5):1429-1435.

Soil respiration constitutes a major component of the global carbon cycle and is likely to be altered by climatic change. However, there is an incomplete understanding of the extent to which various processes contribute to total soil respiration, especially the contributions of root and rhizosphere respiration. Here, using a stable carbon isotope tracer, we separate the relative contributions of root and soil heterotrophic respiration to total soil respiration in situ. The Free-Air Carbon dioxide Enrichment (FACE) facility in the Duke University Forest (NC) fumigates plots of an undisturbed loblolly pine (*Pinus taeda* L.) forest with CO₂ that is strongly depleted in C-13. This labeled CO₂ is found in the soil pore space through live root and mycorrhizal respiration and soil heterotroph respiration of labile root exudates. By measuring the depletion of (CO₂)-C-13 in the soil system, we found that the rhizosphere contribution to soil CO₂ reflected the distribution of fine roots in the soil and that late in the growing season roots contributed 55% of total soil respiration at the surface. This estimate may represent an upper limit on the contribution of roots to soil respiration because high atmospheric CO₂ often increases in root density and/or root activity in the soil.

KEYWORDS: CO₂, DECIDUOUS FOREST, FATE, FLUXES, LITTER, ORGANIC-MATTER, PONDEROSA PINE, RHIZOSPHERE, SEEDLINGS

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Andrews, T.J., G.S. Hudson, C.J. Mate, S. Voncaemmerer, J.R. Evans, and Y.B.C. Arvidsson. 1995. Rubisco - the consequences of altering its expression and activation in transgenic plants. *Journal of Experimental Botany* 46:1293-1300.

Transgenic tobacco (*Nicotiana tabacum* W38) hemizygous for a single antisense gene directed against Rubisco's small subunit had 35% of the Rubisco content of control leaves (15% when homozygous). CO₂ assimilation (at 1000 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) and 350 $\mu\text{bar CO}_2$) by the hemizygous leaves was reduced to 40% of that of the controls without material effect on stomatal conductance, chlorophyll content or other photosynthetic components. Leaf soluble protein was reduced commensurately with the reduction in Rubisco. CO₂ assimilation rate in the hemizygous leaves remained limited by Rubisco activity at all, even very high, CO₂ concentrations. This led to a simple, hyperbolic response of photosynthesis to intraplasmid CO₂ concentration from which the in vivo catalytic properties of Rubisco were inferred and compared with those of isolated Rubisco in vitro. Using a similar approach, the content of Rubisco activase was suppressed by incorporating a partial cDNA for activase into the tobacco genome in the antisense orientation with respect to a cauliflower mosaic virus 35S promoter. The progeny of a primary transformant with two anti-activase inserts had from <1% to 20% of the activase content of control plants. Quite severe suppression of activase, to less than 5% of the amount present in control leaves, was required before effects on photosynthesis and growth became apparent, indicating that one activase tetramer must be able to service, continuously, as many as 200 Rubisco octamers. Plants with lower activase contents could not grow unless the atmosphere was enriched with CO₂. Their Rubisco was less carbamylated and they had lower CO₂ assimilation rates than the controls. The rate of release of 2'-carboxyarabinitol-1-phosphate from Rubisco after illumination of the anti-activase leaves was also impaired. Older anti-activase plants accumulated increasing amounts of Rubisco in their younger leaves, but were unable to carbamylate it. The photosynthetic rate per carbamylated Rubisco active site in the strongly suppressed anti-activase leaves was only approximately 25% of that seen in control leaves, suggesting that activase may not only promote carbamylation of uncarbamylated Rubisco sites, but also accelerate turnover at carbamylated sites.

KEYWORDS: 2-CARBOXYARABINITOL 1-PHOSPHATE, ACTIVITY INVIVO, ANTISENSE GENE, CATALYSIS, GROWTH,

PHOTOSYNTHESIS, RIBULOSE BIPHOSPHATE CARBOXYLASE, RIBULOSE-1,5-BIPHOSPHATE CARBOXYLASE-OXYGENASE, SLOW INACTIVATION, TOBACCO NICOTIANA-TABACUM

56

Andriolo, J.L., J. LeBot, C. Gary, G. Sappe, P. Orlando, B. Brunel, and C. Sarrouy. 1996. An experimental set-up to study carbon, water and nitrate uptake rates by hydroponically grown plants. *Journal of Plant Nutrition* 19(10-11):1441-1462.

The experimental system described allows concomitant hourly measurements of CO₂, H₂O, and NO₃ uptake rates by plants grown hydroponically in a greenhouse. Plants are enclosed in an airtight chamber through which air flows at a controlled speed. Carbon dioxide exchange and transpiration rates are determined from respective differences of concentrations of CO₂ and water vapor of the air at the system inlet and outlet. This set-up is based on the "open-system" principle with improvements made on existing systems. For instance, propeller anemometers are used to monitor air flow rates in the chamber. From their signal it is possible to continuously adjust air speed to changing environmental conditions and plant activity. The air temperature inside the system therefore never rises above that outside. Water and NO₃ uptake rates are calculated at time intervals from changes in the volume and the NO₃ concentration of the nutrient solution in contact with the roots. The precise measurement of the volume of solution is achieved using a balance which has a higher precision than any liquid level sensors. Nitrate concentration is determined in the laboratory from aliquots of solution sampled at time intervals. A number of test runs are reported which validate the measurements and confirm undisturbed conditions within the system. Results of typical diurnal changes in CO₂, H₂O, and NO₃ uptake rates by fruiting tomato plants are also presented.

KEYWORDS: CROP, DIOXIDE, ELEVATED CO₂, GAS-EXCHANGE, LIFE-CYCLE, OPEN-TOP CHAMBERS, PHOTOSYNTHESIS, SYSTEM, TOMATO, TRANSPIRATION

57

Angell, R., and T. Svejcar. 1999. A chamber design for measuring net CO₂ exchange on rangeland. *Journal of Range Management* 52(1):27-31.

Net carbon exchange of terrestrial ecosystems will likely change as atmospheric CO₂ concentration increases. Currently, little is known of the annual dynamics or magnitude of CO₂ flux on many native and agricultural ecosystems. Remoteness of many ecosystems has limited our ability to measure CO₂ flux on undisturbed vegetation. Today, many plant ecologists have portable photosynthesis systems with which they make single-leaf photosynthesis measurements. Utility of this equipment is enhanced when canopy-level CO₂ flux is also measured. We designed a portable 1-m³ closed chamber for use in measuring CO₂ exchange in short statured vegetation with widely varied canopy structure. The design includes external ductwork equipped with doors which are used to open the chamber for ventilation with outside air between measurements. The chamber was tested on a Wyoming big sagebrush (*Artemisia tridentata* ssp. *Wyomingensis* Nutt.)/Thurber's needlegrass (*Stipa thurberiana* Piper) community using 10 plots equally divided between shrub and interspace. The ductwork and doors provided adequate ventilation to allow consecutive measurements of CO₂ flux without removing the chamber from the plot. The chamber could differentiate CO₂ flux between plots with sagebrush and those with grass only, even at relatively low fluxes. Net CO₂ uptake per unit ground area was greater ($P = 0.04$) on sagebrush-grass plots (7.6 \pm 1.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$) than on interspace plots without sagebrush (3.1 \pm 1.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Chamber and leaf temperature increased by an average of 0.5 and 1.2 degrees C, respectively, during measurements.

KEYWORDS: CARBON-CYCLE, FLUXES, SYSTEM, TUNDRA ECOSYSTEMS

58

Apel, P., and M. Peisker. 1995. Variability of photosynthetic gas exchange parameters, dark respiration, and stomatal numbers in species of Polygonum. *Physiologia Plantarum* 95(3):365-372.

Within the genus Polygonum a large variation was found between species with regard to stomatal number, gas phase resistance, intracellular resistance and dark respiration. Interspecific variation in CO₂ compensation concentration and intercellular CO₂ concentration at constant external concentration were comparatively small. Correlations were found between stomatal number and gas phase resistance, stomatal number and Gamma, and Gamma and the product of dark respiration rate and intracellular resistance. The influence of dark respiration and stomatal number on photosynthetic gas exchange is discussed. It was concluded that dark respiration in light was enhanced by 22% as a mean value in 9 Polygonum species and by 62% in Polygonum lapathifolium.

KEYWORDS: CONDUCTANCE, LEAVES, PLANTS

59

Apple, M.E., M.S. Lucash, D.M. Olszyk, and D.T. Tingey. 1998. Morphogenesis of Douglas-fir buds is altered at elevated temperature but not at elevated CO₂. *Environmental and Experimental Botany* 40(2):159-172.

Global climatic change as expressed by increased CO₂ and temperature has the potential for dramatic effects on trees. To determine what its effects may be on Pacific Northwest forests, Douglas-fir (*Pseudotsuga menziesii*) seedlings were grown in sun-lit controlled environment chambers at ambient or elevated (+ 4 degrees C above ambient) temperature, and at ambient or elevated (+ 200 ppm above ambient) CO₂. In 1995-1996 and 1996- 1997, elevated CO₂ had no effect on vegetative bud morphology, while the following unusual morphological characteristics were found with greater frequency at elevated temperature than at ambient: rosetted buds with reflexed and loosened outer scales, convoluted inner scales, clusters of small buds, needles elongating between scales, needle primordia with white, hyaline apical extensions, and buds with hardened scales inside of unbroken buds. Buds became rosetted in elevated temperature chambers after temperatures exceeded 40 degrees C in July, 1996. Rosettes were induced within 48-h in buds placed in a 40 degrees C oven; fewer rosettes formed at 20 degrees C. Induction was reversible in buds transferred from 40 to 20 degrees C, implying that resetting is a physical rather than a growth phenomenon. It appears that rosettes form after long- term exposure to elevated temperature and after shorter periods of exposure to intense heat. Elevated temperature influences bud morphology and may therefore influence the overall branching structure of Douglas-fir seedlings. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ACCUMULATION, BUDBURST, CHILLING REQUIREMENT, DORMANCY, FROST DAMAGE, HEAT-SHOCK PROTEINS, INTERIOR, POPULATIONS, SEEDLINGS, SHOOT

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Arakelyan, V.V., G.B. Ibragimova, and Y.S. Nasyrov. 1993. Effects of light, CO₂, and temperature on carbonic-anhydrase activity in C₃-plants. *Russian Journal of Plant Physiology* 40(6):759-767.

Carbonic anhydrase activity was studied in cotton (*Gossypium hirsutum* L.) and Triticale plants exposed to various light intensities, temperatures, and CO₂ concentrations in the air. The activity was measured using an

original method based on the HCO₃⁻ dehydration reaction, which is carried out in conditions resembling those occurring in the chloroplast stroma in vivo. Carbonic anhydrase activity in stromal fractions from cotton and triticale plant chloroplasts appears to respond to environmental changes. Plant exposure to increased light intensities and temperatures results in increased activity, whereas high ambient CO₂ concentrations lower carbonic anhydrase activity. After examining in vitro the HCO₃⁻ dehydration reaction, which in vivo is catalyzed by carbonic anhydrase, we concluded that the physiological role of the stromal enzyme consists of preventing local CO₂ depletion in the carboxylation sites. Thus, high temperatures and low ambient CO₂ concentrations enhance carbonic anhydrase activity, while impeding CO₂ transport from the air to the carboxylation sites in the leaf. This accelerates HCO₃⁻ dehydration and reduces its concentration in the stroma, thereby producing an additional driving force for HCO₃⁻ transport to the chloroplast.

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Archer, S., D.S. Schimel, and E.A. Holland. 1995. Mechanisms of shrubland expansion - land-use, climate or CO₂. *Climatic Change* 29(1):91-99.

Encroachment of trees and shrubs into grasslands and the 'thicketization' of savannas has occurred worldwide over the past century. These changes in vegetation structure are potentially relevant to climatic change as they may be indicative of historical shifts in climate and as they may influence biophysical aspects of land surface-atmosphere interactions and alter carbon and nitrogen cycles. Traditional explanations offered to account for the historic displacement of grasses by woody plants in many arid and semi-arid ecosystems have centered around changes in climatic, livestock grazing and fire regimes. More recently, it has been suggested that the increase in atmospheric CO₂ since the industrial revolution has been the driving force. In this paper we evaluate the CO₂ enrichment hypotheses and argue that historic, positive correlations between woody plant expansion and atmospheric CO₂ are not cause and effect.

KEYWORDS: AMERICAN SOUTHWEST, ATMOSPHERIC CO₂, CARBON DIOXIDE, DESERTIFICATION, ECOSYSTEMS, ELEVATED CO₂, GROWTH, INCREASING CO₂, NATURAL VEGETATION, PAST 2 CENTURIES

62

Arienzo, M., G. Basile, R. Dandria, V. Magliulo, and A. Zena. 1995. Irrigation with carbonated water and nutrient availability - tests on strawberry plants. *Agrochimica* 39(1):61-72.

A research was carried out to study the nutrient availability and yield performances of a strawberry crop cv. 'Chandler' in response to equivalent depths (100% of ETM) of CO₂ enriched water and plain water applied with different irrigation frequencies. Plots were arranged in a complete randomized block design replicated four times, using mulch and a drip irrigation system adopting 4 l/h emitters. The crop was covered by a plastic tunnel following treatment differentiation. The statistical analysis revealed an increased availability of Cu, Zn, Ca, Mg, and Mn for the CO₂ treatment, probably linked with the pH reduction (from 7.5 to 6.5). The increased nutrient uptake in the CO₂ enriched water treatment may be the cause of the commercial yield enhancement (8.6 %) and reduction in the weight of deformed berries (-12.1 %).

KEYWORDS: DIOXIDE

63

Arisi, A.C.M., G. Cornic, L. Jouanin, and C.H. Foyer. 1998.

Overexpression of iron superoxide dismutase in transformed poplar modifies the regulation of photosynthesis at low CO₂ partial pressures or following exposure to the prooxidant herbicide methyl viologen. *Plant Physiology* 117(2):565-574.

Chloroplast-targeted overexpression of an Fe superoxide dismutase (SOD) from *Arabidopsis thaliana* resulted in substantially increased foliar SOD activities. Ascorbate peroxidase, glutathione reductase, and monodehydroascorbate reductase activities were similar in the leaves from all of the lines, but dehydroascorbate reductase activity was increased in the leaves of the FeSOD transformants relative to untransformed controls. Foliar H₂O₂, ascorbate, and glutathione contents were comparable in all lines of plants. Irradiance-dependent changes in net CO₂, assimilation and chlorophyll a fluorescence quenching parameters were similar in all lines both in air (21% O₂) and at low (1%) O₂. CO₂-response curves for photosynthesis showed similar net CO₂-exchange characteristics in all lines. In contrast, values of photochemical quenching declined in leaves from untransformed controls at intercellular CO₂ (C_i) values below 200 μmol L⁻¹ but remained constant with decreasing C_i in leaves of FeSOD transformants. When the O₂ concentration was decreased from 21 to 1%, the effect of FeSOD overexpression on photochemical quenching at limiting C_i was abolished. At high light (1000 μmol m⁻² s⁻¹) a progressive decrease in the ratio of variable (F_v) to maximal (F_m) fluorescence was observed with decreasing temperature. At 6 degrees C the high-light-induced decrease in the F_v/F_m ratio was partially prevented by low O₂ but values were comparable in all lines. Methyl viologen caused decreased F_v/F_m ratios, but this was less marked in the FeSOD transformants than in the untransformed controls. These observations suggest that the rate of superoxide dismutation limits flux through the Mehler-peroxidase cycle in certain conditions.

KEYWORDS: ASCORBATE PEROXIDASE, CHLOROPHYLL FLUORESCENCE, ELEVATED LEVELS, HYDROGEN- PEROXIDE, OXIDATIVE STRESS TOLERANCE, PHOTONHIBITION, QUANTUM YIELD, SPINACH-CHLOROPLASTS, TEMPERATURE, TRANSGENIC PLANTS

64

Arnone, J.A. 1997. Indices of plant N availability in an alpine grassland under elevated atmospheric CO₂. *Plant and Soil* 190(1):61-66.

The objective of this study was to estimate whether elevated atmospheric [CO₂] alters plant N availability in a native high- elevation grassland in the Swiss Alps using two integrative, relatively non-disruptive methods. Estimates based on seasonal net plant N uptake, and those based on the amounts of NH₄⁺-N plus NO₃⁻-N captured by ion exchange resin (IER) bags, did not differ in plots treated with ambient (355 μmol L⁻¹) and elevated (680 μmol L⁻¹) [CO₂] in either the second (1993) or third (1994) growing season under treatment with elevated [CO₂]. The results of this study suggest that the effects of rising atmospheric [CO₂] on plant N availability may be negligible in this grassland. The results also contrast the relatively large effects of elevated atmospheric [CO₂] (increases and decreases) reported for highly disturbed artificial systems.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, EXCHANGE, FEEDBACK, GROWTH FORMS, NITROGEN-AVAILABILITY, NUTRIENT AVAILABILITY, RESPONSES, SOIL-NITROGEN, TUNDRA

65

Arnone, J.A. 1997. Temporal responses of community fine root populations to long- term elevated atmospheric CO₂ and soil nutrient patches in model tropical ecosystems. *Acta Oecologica-International Journal of Ecology* 18(3):367-376.

Biomass and length density of fine roots, as well as overall allocation of

dry matter to root growth, of C-3 plants has been shown to increase under elevated CO₂. However, it is uncertain whether the stimulatory effect of elevated CO₂ on fine root population size in plant communities will persist, or whether fine root populations at high CO₂ simply reach their maximum sooner (or possibly later) than those produced under ambient CO₂. It is also unclear whether increased nutrient demand at the stand-level under elevated CO₂ will lead to more intense nutrient foraging via enhanced fine root proliferation into relatively nutrient-rich soil microsites. I addressed these questions in a 530 day experiment with model tropical plant communities established in four equivalent ecosystem (17 m²) in which plants shared a common low fertility soil. Fine root (less than or equal to 2 mm empty set) populations (biomass and length density) in ecosystems maintained at elevated CO₂ (610 μmol l⁻¹) increased more rapidly than those in ecosystems maintained at ambient CO₂ (340 μmol l⁻¹) during the first half of the experiment and also remained greater over the entire experiment. The data also indicate that: (1) fine root populations at both CO₂ levels eventually stabilize, (2) stabilization occurs sooner under elevated CO₂ (occupation of the soil volume), and (3) steady-state populations under elevated CO₂ may be slightly larger than those maintained under ambient CO₂. Fine root proliferation into artificially nutrient- enriched microsites was dramatic in all ecosystems (22% to 75% greater than into non-enriched soil). However, proliferation into enriched microsites was not enhanced by elevated CO₂. Thus, elevated CO₂ may not enhance exploitation of nutrient- rich microsites even in low fertility soils, suggesting that increased plant nutrient capture under elevated CO₂ also may be unlikely.

KEYWORDS: AMAZONIAN FORESTS, BIOMASS, CARBON DIOXIDE, ENRICHMENT, GROWTH, MICROSITES, PLANT-COMMUNITIES, PROLIFERATION, RAIN-FOREST, UPTAKE KINETICS

66

Arnone, J.A. 1999. Symbiotic N₂ fixation in a high Alpine grassland: effects of four growing seasons of elevated CO₂. *Functional Ecology* 13(3):383-387.

1. Increasing carbon dioxide concentration (E: 680 μmol CO₂ litre⁻¹) vs ambient, A: 355 μmol CO₂ litre⁻¹) around late- successional Alpine sedge communities of the Swiss Central Alps (2450 m) for four growing seasons (1992-1995) had no detectable effect on symbiotic N₂ fixation in *Trifolium alpinum*-the sole N₂-fixing plant species in these communities (74 ± 30 mg N m⁻² year⁻¹, A and E plots pooled). 2. This result is based on data collected in the fourth growing season showing that elevated CO₂ had no effect on *Trifolium* above-ground biomass (4.4 ± 1.7 g m⁻², A and E plots pooled, n = 24) or N content per unit land area (124 ± 51 mg N m⁻², A and E pooled), or on the percentage of N *Trifolium* derived from the atmosphere through symbiotic N₂ fixation (%Ndfa: 61.0 ± 4.1 across A and E plots) estimated using the N-15 dilution method. 3. Thus, it appears that N inputs to this ecosystem via symbiotic N₂ fixation will not be dramatically affected in the foreseeable future even as atmospheric CO₂ continues to rise.

KEYWORDS: ATMOSPHERIC CO₂, ECOSYSTEM, ENRICHMENT, GAS-EXCHANGE, NITROGENASE ACTIVITY, NODULATION, REDUCTION, RESPONSES, TRIFOLIUM-REPENS L, TUNDRA

67

Arnone, J.A., and P.J. Bohlen. 1998. Stimulated N₂O flux from intact grassland monoliths after two growing seasons under elevated atmospheric CO₂. *Oecologia* 116(3):331-335.

Long-term exposure of native vegetation to elevated atmospheric CO₂ concentrations is expected to increase C inputs to the soil and, in

ecosystems with seasonally dry periods, to increase soil moisture. We tested the hypothesis that these indirect effects of elevated CO₂ (600 μmol(-1) vs 350 μmol(-1)) would improve conditions for microbial activity and stimulate emissions of nitrous oxide (N₂O), a very potent and long-lived greenhouse gas. After two growing seasons, the mean N₂O efflux from monoliths of calcareous grassland maintained at elevated CO₂ was twice as high as that measured from monoliths maintained at current ambient CO₂ (70 ± 9 vs 37 ± 4 μmol N₂O m⁻² h⁻¹) in October, 27 ± 5 vs 13 ± 3 μmol N₂O m⁻² h⁻¹) in November after aboveground harvest). The higher N₂O emission rates at elevated CO₂ were associated with increases in soil moisture, soil heterotrophic respiration, and plant biomass production, but appear to be mainly attributable to higher soil moisture. Our results suggest that rising atmospheric CO₂ may contribute more to the total greenhouse effect than is currently estimated because of its plant-mediated effects on soil processes which may ultimately lead to increased N₂O emissions from native grasslands.

KEYWORDS: CALCAREOUS GRASSLAND, CARBON-DIOXIDE ENRICHMENT, DENITRIFICATION, ECOSYSTEMS, INCREASE, METHANE, NITROUS-OXIDE PRODUCTION, SHORTGRASS STEPPE, SOIL-NITROGEN, STOMATAL RESPONSES

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Arnone, J.A., and J.C. Gordon. 1990. Effect of nodulation, nitrogen-fixation and CO₂ enrichment on the physiology, growth and dry mass allocation of seedlings of *alnus-rubra* bong. *New Phytologist* 116(1):55-66.

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Arnone, J.A., and G. Hirschel. 1997. Does fertilizer application alter the effects of elevated CO₂ on *Carex* leaf litter quality and in situ decomposition in an alpine grassland? *Acta Oecologica-International Journal of Ecology* 18(3):201-206.

The purpose of our investigation was to determine: (1) whether fertilization with NPK would result in an improvement in leaf litter quality of the dominant species (*Carex curvula*) in a high alpine grassland in Switzerland; and especially (2) if fertilization improves the quality of leaf litter produced under elevated atmospheric CO₂ and compensates for the suppressive effects of high CO₂ on the in situ decomposition rates of *C. curvula* litter, observed at this site in an earlier study. Fertilizer application (40 kg N ha⁻¹ yr⁻¹) resulted in 34% higher leaf litter [N] but did not change C:N or lignin N ratios, when viewed across both CO₂ treatments. Improvement in the mean N quality of litter produced under elevated CO₂ resulting from fertilization appeared to lead to a significantly faster mean decomposition rate (+60%), but fertilization had no significant effect on decomposition of litter produced under ambient CO₂. We conclude that the potential stimulatory effect of an increase in atmospheric N deposition on litter quality and decomposition rates may partially compensate for the inhibitory effects of rising atmospheric CO₂ in these high alpine grassland ecosystems.

KEYWORDS: ECOSYSTEMS, NITROGEN, RESPONSES

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Arnone, J.A., and C. Kestenholtz. 1997. Root competition and elevated CO₂: Effects on seedling growth in *Linum usitatissimum* populations and *Linum Silene cretica* mixtures. *Functional Ecology* 11(2):209-214.

1. Root competition can be an important determinant of the performance of neighbours within plant populations and communities. Because plants often maintain larger root systems and allocate more of their carbon to root systems under elevated atmospheric CO₂ than they do at lower CO₂

concentrations, root-root interactions could play an increasingly important role in determining competitive outcomes among individuals and plant species as global CO₂ concentration continues to rise. 2. We established 12 pure stands of *Linum usitatissimum* (flax) and 12 mixed stands of *Linum* and its naturally co-occurring weed species *Silene cretica* in opaque plastic trays each filled with the same amount of nutrient-rich soil mix. In half of the trays from each of these stand types, vertical waterproof partitions separated the root systems of individual plants from each other to prevent root competition, while in the other half no partitions were present. Half of the trays from all treatments were allowed to grow under low atmospheric CO₂ concentration (320 μmol(-1)) and the other half under elevated CO₂ (600 μmol(-1)), in daylight growth chambers for 30 days from seedling emergence until harvest in mid-June. All trays received equal amounts of water so that soils in the low CO₂ treatment were maintained at field capacity. 3. Our results indicate that under high soil fertilities: (1) intra-specific root-root interactions alone play a relatively insignificant role in determining plant biomass production within pure *Linum* populations and (2) the impact of an aggressive species (*Silene*) on co-occurring less aggressive species (*Linum*) becomes more severe under elevated CO₂ as a result of amplified interspecific root competition.

KEYWORDS: AMBIENT, ANNUALS, ATMOSPHERIC CO₂, C-3, CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ENRICHMENT, PLANTS, RESPONSES

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Arnone, J.A., and C. Korner. 1993. Influence of elevated CO₂ on canopy development and red - far-red ratios in 2-storied stands of *ricinus-communis*. *Oecologia* 94(4):510-515.

Vertical structure of plant stands and canopies may change under conditions of elevated CO₂ due to differential responses of overstory and understory plants or plant parts. In the long term, seedling recruitment, competition, and thus population or community structure may be affected. Aside from the possible differential direct effects of elevated CO₂ on photosynthesis and growth, both the quantity and quality of the light below the overstory canopy could be indirectly affected by CO₂-induced changes in overstory leaf area index (LAI) and/or changes in overstory leaf quality. In order to explore such possible interactions, we compared canopy leaf area development, canopy light extinction and the quality of light beneath overstory leaves of two-storied monospecific stands of *Ricinus communis* exposed to ambient (340 μmol(-1)) and elevated (610 μmol(-1)) CO₂. Plants in each stand were grown in a common soil as closed "artificial ecosystems" with a ground area of 6.7 m². LAI of overstory plants in all ecosystems more than doubled during the experiment but was not different between CO₂ treatments at the end. As a consequence, extinction of photosynthetically active radiation (PAR) was also not altered. However, under elevated CO₂ the red to far-red ratio (R:FR) measured beneath overstory leaves was 10% lower than in ecosystems treated with ambient CO₂. This reduction was associated with increased thickness of palisade layers of overstory leaves and appears to be a plausible explanation for the specific enhancement of stem elongation of understory plants (without a corresponding biomass response) under elevated CO₂. Col enrichment led to increased biomass of overstory plants (mainly stem biomass) but had no effect on understory biomass. The results of this study raise the possibility of an important indirect effect of elevated CO₂ at the stand-level. We suggest that, under elevated CO₂, reductions in the R:FR ratio beneath overstory canopies may affect understory plant development independently of the effects of PAR extinction.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL CONTENT, CLOVER TRIFOLIUM-REPENS, GROWTH, LEAF ANATOMY, LIGHT-QUALITY, PLANTS, RAIN-FOREST, RESPONSES

Arnone, J.A., and C. Korner. 1995. Soil and biomass carbon pools in model communities of tropical plants under elevated CO₂. *Oecologia* 104(1):61-71.

The experimental data presented here relate to the question of whether terrestrial ecosystems will sequester more C in their soils, litter and biomass as atmospheric CO₂ concentrations rise. Similar to our previous study with relatively fertile growth conditions (Korner and Arnone 1992), we constructed four rather nutrient-limited model communities of moist tropical plant species in greenhouses (approximately 7 m² each). Plant communities were composed of seven species (77 individuals per community) representing major taxonomic groups and various life forms found in the moist tropics. Two ecosystems were exposed to 340 μmol CO₂ l⁻¹ and two to 610 μmol l⁻¹ for 530 days of humid tropical growth conditions. In order to permit precise determination of C deposition in the soil, plant communities were initially established in C-free unwashed quartz sand. Soils were then amended with known amounts of organic matter (containing C and nutrients). Mineral nutrients were also supplied over the course of the experiment as timed-release full-balance fertilizer pellets. Soils represented by far the largest repositories for fixed C in all ecosystems. Almost 5 times more C (ca. 80% of net C fixation) was sequestered in the soil than in the biomass, but this did not differ between CO₂ treatments. In addition, at the whole-ecosystem level we found a remarkably small and statistically non-significant increase in C sequestration (+4%; the sum of C accretion in the soil, biomass, litter and necromass). Total community biomass more than quadrupled during the experiment, but at harvest was, on average, only 8% greater (i.e. 6% per year; n.s.) under elevated CO₂, mainly due to increased root biomass (+15%, P = 0.12). Time courses of leaf area index of all ecosystems suggested that canopy expansion was approaching steady state by the time systems were harvested. Net primary productivity (NPP) of all ecosystems - i.e. annual accumulation of biomass, necromass, and leaf litter (but not plant-derived soil organic matter) - averaged 815 and 910 g m⁻² year⁻¹ at ambient and elevated CO₂, respectively. These NPPs are remarkably similar to those of many natural moist tropical forested ecosystems. At the same time net productivity of soil organic matter reached 7000 g dry matter equivalent per m² and year (i.e. 3500 g C m⁻² year⁻¹). Very slight yet statistically significant CO₂-induced shifts in the abundance of groups of species occurred by the end of the experiment, with one group of species (*Elettaria cardamomum*, *Ficus benjamina*, *F. pumila*, *Epipremnum pinnatum*) gaining slightly, and another group (*Ctenanthe lubbersiana*, *Heliconia humilis*, *Cecropia peltata*) losing. Our results show that: (1) enormous amounts of C can be deposited in the ground which are normally not accounted for in estimates of NPP and net ecosystem productivity; (2) any enhancement of C sequestration under elevated atmospheric CO₂ may be substantially smaller than is believed will occur (yet still very important), especially under growth conditions which permit close to natural NPP; and (3) species dominance in plant communities is likely to change under elevated CO₂, but that changes may occur rather slowly.

KEYWORDS: AMBIENT, ATMOSPHERIC CO₂, C-3, COMPETITION, DIOXIDE, ENRICHMENT, ESTUARINE MARSH, GROWTH, NITROGEN, TUSSOCK TUNDRA

Arnone, J.A., J.G. Zaller, C. Ziegler, H. Zandt, and C. Korner. 1995. Leaf quality and insect herbivory in model tropical plant-communities after long-term exposure to elevated atmospheric CO₂. *Oecologia* 104(1):72-78.

Results from laboratory feeding experiments have shown that elevated atmospheric carbon dioxide can affect interactions between plants and insect herbivores, primarily through changes in leaf nutritional quality occurring at elevated CO₂. Very few data are available on insect

herbivory in plant communities where insects can choose among species and positions in the canopy in which to feed. Our objectives were to determine the extent to which CO₂-induced changes in plant communities and leaf nutritional quality may affect herbivory at the level of the entire canopy. We introduced equivalent populations of fourth instar *Spodoptera eridania*, a lepidopteran generalist, to complex model ecosystems containing seven species of moist tropical plants maintained under low mineral nutrient supply. Larvae were allowed to feed freely for 14 days, by which time they had reached the seventh instar. Prior to larval introductions, plant communities had been continuously exposed to either 340 μmol CO₂ l⁻¹ or to 610 μmol l⁻¹ for 1.5 years. No major shifts in leaf nutritional quality [concentrations of N, total non-structural carbohydrates (TNC), sugar, and starch; ratios of: C/N, TNC/N, sugar/N, starch/N; leaf toughness] were observed between CO₂ treatments for any of the species. Furthermore, no correlations were observed between these measures of leaf quality and leaf biomass consumption. Total leaf area and biomass of all plant communities were similar when caterpillars were introduced. However, leaf biomass of some species was slightly greater - and for other species slightly less (e.g. *Cecropia peltata*) - in communities exposed to elevated CO₂. Larvae showed the strongest preference for *C. peltata* leaves, the plant species that was least abundant in all communities, and fed relatively little on plants species which were more abundant. Thus, our results indicate that leaf tissue quality, as described by these parameters, is not necessarily affected by elevated CO₂ under relatively low nutrient conditions. Hence, the potential importance of CO₂-induced shifts in leaf nutritional quality, as determinants of herbivory, may be overestimated for many plant communities growing on nutrient-poor sites if estimates are based on traditional laboratory feeding studies. Finally, slight shifts in the abundance of leaf tissue of various species occurring under elevated CO₂ will probably not significantly affect herbivory by generalist insects. However, generalist insect herbivores appear to become more dependent on less-preferred plant species in cases where elevated CO₂ results in reduced availability of leaves of a favoured plant species, and this greater dependency may eventually affect insect populations adversely.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ATMOSPHERES, CHLOROPHYLL CONTENT, ECOSYSTEMS, ENRICHMENT, FOREST, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, RESPONSES

Arp, W.J. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant, Cell and Environment* 14(8):869-875.

While photosynthesis of C₃ plants is stimulated by an increase in the atmospheric CO₂ concentration, photosynthetic capacity is often reduced after long-term exposure to elevated CO₂. This reduction appears to be brought about by end product inhibition, resulting from an imbalance in the supply and demand of carbohydrates. A review of the literature revealed that the reduction of photosynthetic capacity in elevated CO₂ was most pronounced when the increased supply of carbohydrates was combined with small sink size. The volume of pots in which plants were grown affected the sink size by restricting root growth. While plants grown in small pots had a reduced photosynthetic capacity, plants grown in the field showed no reduction or an increase in this capacity. Pot volume also determined the effect of elevated CO₂ on the root/shoot ratio: the root/shoot ratio increased when root growth was not restricted and decreased in plants grown in small pots. The data presented in this paper suggest that plants growing in the field will maintain a high photosynthetic capacity as the atmospheric CO₂ level continues to rise.

KEYWORDS: ATMOSPHERIC CO₂, CARBOHYDRATE CONTENT, CARBON-DIOXIDE ENRICHMENT, CO₂-ENRICHMENT, COTTON

75

Arp, W.J., and B.G. Drake. 1991. Increased photosynthetic capacity of scirpus-olneyi after 4 years of exposure to elevated co2. *Plant, Cell and Environment* 14(9):1003-1006.

While a short-term exposure to elevated atmospheric CO₂ induces a large increase in photosynthesis in many plants, long-term growth in elevated CO₂ often results in a smaller increase due to reduced photosynthetic capacity. In this study, it was shown that, for a wild C3 species growing in its natural environment and exposed to elevated CO₂ for four growing seasons, the photosynthetic capacity has actually increased by 31%. An increase in photosynthetic capacity has been observed in other species growing in the field, which suggests that photosynthesis of certain field grown plants will continue to respond to elevated levels of atmospheric CO₂.

KEYWORDS: ATMOSPHERIC CO₂, C-3, CARBON DIOXIDE, ESTUARINE MARSH, FIELD, INSITU, LEAVES, PLANTS

76

Arp, W.J., B.G. Drake, W.T. Pockman, P.S. Curtis, and D.F. Whigham. 1993. Interactions between C-3 and C-4 salt-marsh plant-species during 4 years of exposure to elevated atmospheric co2. *Vegetatio* 104:133-143.

Elevated atmospheric CO₂ is known to stimulate photosynthesis and growth of plants with the C3 pathway but less of plants with the C4 pathway. An increase in the CO₂ concentration can therefore be expected to change the competitive interactions between C3 and C4 species. The effect of long term exposure to elevated CO₂ (ambient CO₂ concentration + 340 μmol CO₂ mol⁻¹) on a salt marsh vegetation with both C3 and C4 species was investigated. Elevated CO₂ increased the biomass of the C3 sedge *Scirpus olneyi* growing in a pure stand, while the biomass of the C4 grass *Spartina patens* in a monospecific community was not affected. In the mixed C3/C4 community the C3 sedge showed a very large relative increase in biomass in elevated CO₂ while the biomass of the C4 species declined. The C4 grass *Spartina patens* dominated the higher areas of the salt marsh, while the C3 sedge *Scirpus olneyi* was most abundant at the lower elevations, and the mixed community occupied intermediate elevations. *Scirpus* growth may have been restricted by drought and salt stress at the higher elevations, while *Spartina* growth at the lower elevations may be affected by the higher frequency of flooding. Elevated CO₂ may affect the species distribution in the salt marsh if it allows *Scirpus* to grow at higher elevations where it in turn may affect the growth of *Spartina*.

KEYWORDS: COMMUNITIES, COMPETITION, ENRICHMENT, FIELD, GRASS, GROWTH, LIQUIDAMBAR- STYRACIFLUA, PERENNIALS, PINUS-TAEDA SEEDLINGS, STRESS

77

Arp, W.J., J.E.M. Van Mierlo, F. Berendse, and W. Snijders. 1998. Interactions between elevated CO₂ concentration, nitrogen and water: effects on growth and water use of six perennial plant species. *Plant, Cell and Environment* 21(1):1-11.

Two experiments are described in which plants of six species were grown for one full season in greenhouse compartments with 350 or 560 μmol mol⁻¹ CO₂. In the first experiment two levels of nitrogen supply were applied to study the interaction between CO₂ and nitrogen. In the second experiment two levels of water supply were added to the experimental set-up to investigate the three-way interaction between

CO₂, nitrogen and water. Biomass and biomass distribution were determined at harvests, while water use and soil moisture were monitored throughout the experiments. In both experiments a positive effect of CO₂ on growth was found at high nitrogen concentrations but not at low nitrogen concentrations. However, plants used much less water in the presence of low nitrogen concentrations. Drought stress increased the relative effect of elevated CO₂ on growth. Available soil moisture was used more slowly at high CO₂ during drought or at high nitrogen concentrations, while at low nitrogen concentrations decreased water use resulted in an increase in soil moisture. The response to the treatments was similar in all the species used. Although potentially faster growing species appeared to respond better to high CO₂ when supplied with a high level of nitrogen, inherently slow-growing species were more successful at low nitrogen concentrations.

KEYWORDS: ACCLIMATION, C-3, CARBON DIOXIDE, COTTON, DRY-MATTER, ENRICHMENT, HEATHLAND ECOSYSTEMS, NUTRITION, STRESS, YIELD

78

Ashenden, T.W., R. Baxter, and C.R. Rafarel. 1992. An inexpensive system for exposing plants in the field to elevated concentrations of co2. *Plant, Cell and Environment* 15(3):365-372.

An inexpensive, potentially mobile field exposure system is described which may be easily constructed by a small workshop. It may be operated as an open-top with a frustum or covered with a polycarbonate 'lid'. The system is cost-effective for CO₂ exposure work because the small size allows provision of CO₂-enriched atmospheres over prolonged periods at relatively low cost. A preliminary assessment of the chambers has been made and concentrations can be maintained at +/- 6% for a target atmosphere of 680 μmol mol⁻¹ CO₂ under normal operating conditions. Other chamber environmental conditions are reported.

KEYWORDS: AIR-POLLUTION, CHAMBERS

79

Asner, G.P., T.R. Seastedt, and A.R. Townsend. 1997. The decoupling of terrestrial carbon and nitrogen cycles. *BioScience* 47(4):226-234.

KEYWORDS: ATMOSPHERIC CARBON, BIOMASS, CO₂, FOREST ECOSYSTEMS, GLOBAL CHANGE, GRASSLAND, LAND-USE, LONG-TERM, NUTRIENT LIMITATION, SOILS

80

Atkin, O.K., M. Schortemeyer, N. McFarlane, and J.R. Evans. 1999. The response of fast- and slow-growing *Acacia* species to elevated atmospheric CO₂: an analysis of the underlying components of relative growth rate. *Oecologia* 120(4):544-554.

In this study we assessed the impact of elevated CO₂ with unlimited water and complete nutrient on the growth and nitrogen economy of ten woody *Acacia* species that differ in relative growth rate (RGR). Specifically, we asked whether fast- and slow-growing species systematically differ in their response to elevated CO₂. Four slow-growing species from semi-arid environments (*Acacia aneura*, *A. colei*, *A. coriacea* and *A. tetragonophylla*) and six fast-growing species from mesic environments (*Acacia dealbata*, *A. implexa*, *A. mearnsii*, *A. melanoxylon*, *A. irrorata* and *A. saligna*) were grown in glasshouses with either ambient (similar to 350 ppm) or elevated (similar to 700 ppm) atmospheric CO₂. All species reached greater final plant mass with the exception of *A. aneura*, and RGR, averaged across all species, increased by 10% over a 12-week period when plants were exposed to elevated

CO₂. The stimulation of RGR was evident throughout the 12-week growth period. Elevated CO₂ resulted in less foliage area per unit foliage dry mass, which was mainly the result of an increase in foliage thickness with a smaller contribution from greater dry matter content per unit fresh mass. The net assimilation rate (NAR, increase in plant mass per unit foliage area and time) of the plants grown at elevated CO₂ was higher in all species (on average 30% higher than plants in ambient CO₂) and was responsible for the increase in RGR. The higher NAR was associated with a substantial increase in foliar nitrogen productivity in all ten Acacia species. Plant nitrogen concentration was unaltered by growth at elevated CO₂ for the slow-growing Acacia species, but declined by 10% for faster-growing species. The rate of nitrogen uptake per unit root mass was higher in seven of the species when grown under elevated CO₂, and leaf area per unit root mass was reduced by elevated CO₂ in seven of the species. The absolute increase in RGR due to growth under elevated CO₂ was greater for fast- than for slow-growing Acacia species.

KEYWORDS: ALPINE, CARBON DIOXIDE, EFFICIENCY, FOREST, GRASSLAND, LEAF-AREA, NITROGEN ECONOMY, PLANTS, TREES

81

Atkinson, C.J., and J.M. Taylor. 1996. Effects of elevated CO₂ on stem growth, vessel area and hydraulic conductivity of oak and cherry seedlings. *New Phytologist* 133(4):617-626.

Plants of *Quercus robur* L. and *Prunus avium* L. x *P. pseudocerasus* Lind. were grown in either ambient (350 vpm) or elevated (700 vpm) CO₂. The intention was to examine the effects of elevated CO₂ on the morphological and functional development of the stem. The relationships between stem longitudinal transport capacity and development were explored in several ways: stem hydraulic function was related to stem cross-sectional area, supplied leaf area and total stem vessel lumen area. The mean total vessel number and the total vessel lumen area per stem, for both species, was determined from basal sections of the xylem. In *Prunus* seedlings grown in different CO₂ concentrations there was no significant change in the mean vessel size or number of vessels per stem. *Quercus* seedlings grown at elevated CO₂ showed a significant increase in both vessel number and mean vessel size. When total stem vessel area was calculated it had increased twofold for *Quercus* plants grown at elevated CO₂. Measured stem hydraulic conductivity was shown to increase linearly with supplied leaf area, except in *Quercus* seedlings grown at elevated CO₂. Stem hydraulic conductivity for *Quercus* seedlings grown at elevated CO₂ did not change with the increase in supplied leaf area. This absence of an increase in the stem hydraulic conductivity appeared to relate to changes in total stem vessel area. Despite total stem vessel area being greater at elevated CO₂ than that at ambient, it similarly did not increase with supplied leaf area. The implications of this change in the relationship between leaf area and stem hydraulic conductivity are discussed with respect to the possible effects the change might have on the plant's water balance. The possible causes and significance of the changes in xylem anatomy are also considered in relation to direct effects caused by CO₂ or indirect effects on changes in cambial maturity and tree growth.

KEYWORDS: ATMOSPHERIC CO₂, CAVITATION, DIAMETER, EMBOLISM, TRANSPIRATION, TREES, WATER-STRESS, WOODY-PLANTS, XYLEM

82

Atkinson, C.J., J.M. Taylor, D. Wilkins, and R.T. Besford. 1997. Effects of elevated CO₂ on chloroplast components, gas exchange and growth of oak and cherry. *Tree Physiology* 17(5):319-325.

Specific chloroplast proteins, gas exchange and dry matter production in oak (*Quercus robur* L.) seedlings and clonal cherry (*Prunus avium* L.

x *pseudocerasus* Lind.) plants were measured during 19 months of growth in climate-controlled greenhouses at ambient (350 vpm) or elevated (700 vpm) CO₂. In both species, the elevated CO₂ treatment increased the PPFD saturated-rate of photosynthesis and dry matter production. After two months at elevated CO₂, *Prunus* plants showed significant increases in leaf (55%) and stem (61%) dry mass but not in root dry mass. However, this initial stimulation was not sustained: treatment differences in net assimilation rate (A) and plant dry mass were less after 10 months of growth than after 2 months of growth, suggesting acclimation of A to elevated CO₂ in *Prunus*. In contrast, after 10 months of growth at elevated CO₂, leaf dry mass of *Quercus* increased (130%) along with shoot (356%) and root (219%) dry mass, and A was also twice that of plants grown and measured at ambient CO₂. The amounts of Rubisco and the thylakoid-bound protein cytochrome f were higher in *Quercus* plants grown for 19 months in elevated CO₂ than in control plants, whereas in *Prunus* there was less Rubisco in plants grown for 19 months in elevated CO₂ than in control plants. Exposure to elevated CO₂ for 10 months resulted in increased mean leaf area in both species and increased abaxial stomatal density in *Quercus*. There was no change in leaf epidermal cell size in either species in response to the elevated CO₂ treatment. The lack of acclimation of photosynthesis in oak grown at elevated CO₂ is discussed in relation to the production and allocation of dry matter. We propose that differences in carbohydrate utilization underlie the differing long-term CO₂ responses of the two species.

KEYWORDS: ATMOSPHERIC CO₂, BIOCHEMISTRY, CARBON DIOXIDE, LEAF DEVELOPMENT, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, PRUNUS-AVIUM, RESPONSES, TOMATO PLANTS, TREES

83

Atkinson, C.J., P.A. Wookey, and T.A. Mansfield. 1991. Atmospheric-pollution and the sensitivity of stomata on barley leaves to abscisic-acid and carbon-dioxide. *New Phytologist* 117(4):535-541.

Spring barley (*Hordeum vulgare* L. cv. Klaxon) plants were exposed to mixtures of SO₂ + NO₂ (at concentrations of 24-35 nl l⁻¹ of each gas, depending upon fumigation system), or to charcoal-filtered, or unfiltered ambient air during the period in which the second, and subsequent, leaves were emerging. The ability of individual detached leaves to regulate water loss was then examined after terminating the pollutant treatment. Observations of diurnal changes in stomatal resistance of well-watered plants, using a viscous flow porometer, failed to indicate any major alterations which could be attributed to prior exposure to SO₂ + NO₂. By contrast, when an ABA solution (10⁻¹ mol m⁻³) was applied to detached leaves, the stomata of polluted plants were less responsive than plants previously exposed to control air. The dynamics of the observed responses strongly implicated impaired physiology of the guard cells rather than mechanical changes in the epidermis that might, for example, result from damage to the cuticle. Stomatal closure was considerably slower in polluted leaves compared with the controls. This decline in responsiveness to ABA was observed using leaves excised from well-watered plants and in the absence of any externally visible injury. The ability of stomata to respond to a range of CO₂ concentrations from 195-735- μ -mol mol⁻¹ was also examined using individual leaves, attached to the plant, in an environmentally controlled cuvette. Here the stomata of leaves which had been fumigated with SO₂ + NO₂ behaved in a similar manner to the non-fumigated leaves, both showing closure in elevated CO₂ concentrations.

KEYWORDS: CONDUCTANCE, FUMIGATION, NITROGEN-DIOXIDE, NO₂, PLANTS, SO₂, SULFUR-DIOXIDE, SYSTEM, WHEAT LEAVES

84

Austin, M.P. 1992. Modeling the environmental niche of plants - implications for plant community response to elevated CO₂ levels. *Australian Journal of Botany* 40(4-5):615-630.

No simple natural gradients in CO₂ concentration exist for testing predictions about changes in plant communities in response to elevated CO₂. However indirect effects of CO₂ via temperature increases can be tested by reference to natural analogues. Physiologists, vegetation modellers of climate change and community ecologists assume very different temperature responses for plants. Physiologists often assume a skewed non-monotonic curve with a tail towards low temperatures, forest modellers using FORET type models, a symmetric curve, and community ecologists a skewed response with a tail towards high temperatures. These assumptions are reviewed in relation to niche theory, and recent propositions concerning the continuum concept. Confusion exists between the different approaches over the shape of response curves to temperature. Distinctions need to be made between responses due to growth (physiological response), potential fitness (fundamental niche) and observed performance (realised niche). These types of response should be quantified and related to each other if process-models are to be tested for predictive success by reference to naturally occurring communities and temperature gradients. An example of a statistical method for quantifying the realised environmental niche response of a species to temperature is provided. It is based on generalised linear modelling (GLM) of presence/absence data on *Eucalyptus fastigata* for 8377 sites in southern New South Wales, Australia. Seven environmental variables or factors are considered: mean annual temperature, mean annual rainfall, mean monthly solar radiation, topographic position, rainfall seasonality, lithology, and soil nutrient status. The temperature response is modelled with a beta-function, $\log y = a + \alpha \log(t - a) + \delta \log(b - t)$, where t is temperature and letters are parameters. The probability of occurrence is shown to be a skewed function of mean annual temperature. Any process-models of climate change for vegetation incorporating temperature changes due to elevated CO₂ must be capable of generating such realised environmental niche responses for species.

KEYWORDS: DISTRIBUTIONS, ECOSYSTEMS, FIELD, FOREST, GRADIENTS, GROWTH, NORTH-AMERICA, SIMULATION, SPECIES RESPONSE, VEGETATION

85

Awmack, C.S., R. Harrington, and S.R. Leather. 1997. Host plant effects on the performance of the aphid *Aulacorthum solani* (Kalt.) (Homoptera : Aphididae) at ambient and elevated CO₂. *Global Change Biology* 3(6):545-549.

In future elevated CO₂ environments, chewing insects are likely to perform less well than at present because of the effects of increased carbon fixation on their host plants. When the aphid, *Aulacorthum solani* was reared on bean (*Vicia faba*) and tansy (*Tanacetum vulgare*) plants under ambient and elevated CO₂, performance was enhanced on both hosts at elevated CO₂. The nature of the response was different on each plant species suggesting that feeding strategy may influence an insect's response to elevated CO₂. On bean, the daily rate of production of nymphs was increased by 16% but there was no difference in development time, whereas on tansy, development time was 10% shorter at elevated CO₂ but the rate of production of nymphs was not affected. The same aphid clone therefore responded differently to elevated CO₂ on different host plants. This increase in aphid performance could lead to larger populations of aphids in a future elevated CO₂ environment.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, NOCTUIDAE, PHYTOCHEMISTRY, POPULATIONS, RESPONSES

86

Azconbieto, J., M.A. Gonzalezmeler, W. Doherty, and B.G. Drake. 1994. Acclimation of respiratory O₂ uptake in green tissues of field-grown native species after long-term exposure to elevated atmospheric CO₂. *Plant Physiology* 106(3):1163-1168.

C-3 and C-4 plants were grown in open-top chambers in the field at two CO₂ concentrations, normal ambient (ambient) and normal ambient + 340 $\mu\text{L L}^{-1}$ (elevated). Dark oxygen uptake was measured in leaves and stems using a liquid-phase Clark-type oxygen electrode. High CO₂ treatment decreased dark oxygen uptake in stems of *Scirpus olneyi* (C-3) and leaves of *Lindera benzoin* (C-3) expressed on either a dry weight or area basis. Respiration of *Sparfina patens* (C-4) leaves was unaffected by CO₂ treatment. Leaf dry weight per unit area was unchanged by CO₂, but respiration per unit of carbon or per unit of nitrogen was decreased in the C-3 species grown at high CO₂. The component of respiration in stems of *S. olneyi* and leaves of *L. benzoin* primarily affected by long-term exposure to the elevated CO₂ treatment was the activity of the cytochrome pathway. Elevated CO₂ had no effect on activity and capacity of the alternative pathway in *S. olneyi*. The cytochrome c oxidase activity, assayed in a cell-free extract, was strongly decreased by growth at high CO₂ in stems of *S. olneyi* but it was unaffected in *S. patens* leaves. The activity of cytochrome c oxidase and complex III extracted from mature leaves of *L. benzoin* was also decreased after one growing season of plant exposure to elevated CO₂ concentration. These results show that in some C-3 species respiration will be reduced when plants are grown in elevated atmospheric CO₂. The possible physiological causes and implications of these effects are discussed.

KEYWORDS: CARBOHYDRATE STATUS, CARBON-DIOXIDE ENRICHMENT, DARK RESPIRATION, EFFLUX, INHIBITION, LEAF RESPIRATION, LEAVES, PHOTOSYNTHESIS, PLANTS, WORLD

87

Azevedo, R.A., R.M. Alas, R.J. Smith, and P.J. Lea. 1998. Response of antioxidant enzymes to transfer from elevated carbon dioxide to air and ozone fumigation, in the leaves and roots of wild-type and a catalase-deficient mutant of barley. *Physiologia Plantarum* 104(2):280-292.

A catalase-deficient mutant (RPr 794) and the wild-type (cv. Maris Mink) barley (*Hordeum vulgare* L.) counterpart. were grown for 3 weeks in high CO₂ (0.7%) and then transferred to air and ozone (120 nl l^{-1}) in the light and shade for a period of 3 days. Leaves and roots were analysed for catalase (CAT, EC 1.11.1.6), superoxide dismutase (SOD, EC 1.15.1.1) and glutathione reductase (GR, EC 1.6.4.2) activities. CAT activity in the leaves of the RPr 79/4 catalase-deficient mutant was around 5-10% of that determined in Maris Mink. but in the roots, both genotypes contained approximately the same levels of activity. CAT activity in Maris Mink increased in the leaves after transferring plants from 0.7% CO₂ to air or ozone, reaching a maximum of 5-fold. after 4 days in shade and ozone. For the catalase-deficient mutant. only small increases in CAT activity were observed in light/air and light/ozone treatments. In the roots. CAT activity decreased consistently in both genotypes, after plants were transferred from 0.7% CO₂. The total soluble SOD activity in the leaves and roots of both genotypes increased after plants were transferred from 0.7% CO₂. The analysis of SOD isolated from leaves following non-denaturing PAGE, revealed the presence of up to eight SOD isoenzymes classified as Mn-SOD or Cu/Zn-SODs: Fr-SOD was not detected. Significant changes in Mn- and Cu/Zn-SOD isoenzymes were observed; however, they could not account for the increase in total SOD activity. In leaves. GR activity also increased in Maris Mink and RPr 79/4, following transfer from 0.7% CO₂: however, no constant pattern could be established, while in roots, GR activity was reduced after 4 days of the treatments. The data suggest that elevated CO₂ decreases oxidative stress in barley leaves and that soluble CAT and SOD activities increased rapidly after plants were

transferred from elevated CO₂. irrespective of the treatment (light, shade, air or ozone).

KEYWORDS: ARABIDOPSIS-THALIANA, ASCORBATE PEROXIDASE, DIFFERENTIAL RESPONSE, GLUTAMINE-SYNTHETASE, GLUTATHIONE-REDUCTASE, HORDEUM VULGARE L, NICOTIANA-PLUMBAGINIFOLIA L, OXIDATIVE STRESS, SUPEROXIDE-DISMUTASE, TRANSGENIC TOBACCO

88

Baatrup-Pedersen, A., and T.V. Madsen. 1999. Interdependence of CO₂ and inorganic nitrogen on crassulacean acid metabolism and efficiency of nitrogen use by *Littorella uniflora* (L.) Aschers. *Plant, Cell and Environment* 22(5):535-542.

The hypothesis is tested that crassulacean acid metabolism (CAM) in isoetids is a mechanism which not only conserves inorganic carbon but also plays a role in nitrogen economy of the plants. This hypothesis was tested in an outdoor experiment, where *Littorella uniflora* (L.) Aschers, were grown at two CO₂ and five inorganic nitrogen concentrations in a crossed factorial design. The growth of *Littorella* responded positively to enhanced nitrogen availability at high but not at low CO₂ indicating that growth was limited by nitrogen at high CO₂ only. For the nitrogen-limited plants, the capacity for CAM (CAM(cap)) increased with the degree of nitrogen limitation of growth and an inverse coupling between CAM and tissue-N was found. Although this might indicate a role of CAM in economizing on nitrogen in *Littorella*, the hypothesis was rejected for the following reasons: (1) although CAM(cap) was related to tissue-N no relationship between tissue-N and ambient CAM activity (CAM(ambient)) was found whereas a close relationship would be expected if CAM was regulated by nitrogen availability; (2) the photosynthetic nitrogen use efficiency for high CO₂-grown plants declined with increased CAM(ambient) and with CAM(cap); and (3) growth per unit tissue-N per unit time declined with increased CAM(ambient) and CAM(cap).

KEYWORDS: ACCLIMATION, ACQUISITION, AQUATIC CAM PLANTS, CARBON ASSIMILATION, GROWTH, MACROPHYTES, PHOTOSYNTHETIC PERFORMANCE

89

Bacanamwo, M., and J.E. Harper. 1997. Response of a hypernodulating soybean mutant to increased photosynthate supply. *Plant Science* 124(2):119-129.

Growth chamber studies were conducted to determine if increased photoassimilate supply, through light enhancement and CO₂ enrichment, could reverse the deleterious plant growth and enhance nodule function traits of NOD1-3, a hypernodulating mutant of Williams. Both light enhancement and CO₂ enrichment increased nodule number, acetylene reduction activity plant(-1) (but not specific activity) and dry matter accumulation in all tissues in both genotypes. Total biomass and specific nitrogenase activity were always less in the mutant than in Williams 82, indicating that the inferiority of the mutant may not be reversed by enhanced photoassimilate supply. Under all growth conditions, the mutant allocated relatively more photosynthate to nodules and less photosynthate to roots, compared to the control. Despite this, the decreased growth of the mutant relative to the control was not solely attributable to excessive nodulation of the mutant, since decreased growth was observed even on uninoculated plants. It is suggested that light enhancement and CO₂ enrichment may have stimulated nodulation through increased photosynthate supply, independent of the nodulation autoregulatory signal. (C) 1997 Elsevier Science Ireland Ltd.

KEYWORDS: ACETYLENE-REDUCTION ASSAY, CARBON DIOXIDE,

CULTIVAR ENREI, CV BRAGG, GLYCINE-MAX, NITROGENASE ACTIVITY, NODULATION MUTANTS, ROOT NODULE ACTIVITY, SUPERNODULATING MUTANT, WILD-TYPE

90

Bachelet, D., D. Brown, M. Bohm, and P. Russell. 1992. Climate change in Thailand and its potential impact on rice yield. *Climatic Change* 21(4):347-366.

In Thailand, the world's largest rice exporter, rice constitutes a major export on which the economy of the whole country depends. Climate change could affect rice growth and development and thus jeopardize Thailand's wealth. Current climatic conditions in Thailand are compared to predictions from four general circulation models (GCMs). Temperature predictions correlate well with the observed values. Predictions of monthly rainfall correlate poorly. Virtually all models agree that significant increases in temperature (from 1 to 7-degrees-C) will occur in the region including Thailand following a doubling in atmospheric carbon dioxide (CO₂) concentration. The regional seasonality and extent of the rise in temperature varies with each model. Predictions of changes in rainfall vary widely between models. Global warming should in principle allow a northward expansion of rice-growing areas and a lengthening of the growing season now constrained by low temperatures. The expected increase in water-use efficiency due to enhanced CO₂ might decrease the water deficit vulnerability of dryland rice areas and could make it possible to slightly expand them.

KEYWORDS: AMBIENT

91

Bachelet, D., and C.A. Gay. 1993. The impacts of climate change on rice yield - a comparison of 4 model performances. *Ecological Modelling* 65(1-2):71-93.

Increasing concentrations of carbon dioxide (CO₂) and other greenhouse gases are expected to modify the climate of the earth in the next 50-100 years. Mechanisms of plant response to these changes need to be incorporated in models that predict crop yield estimates to obtain an understanding of the potential consequences of such changes. This is particularly important in Asia where demographic forecasts indicate that rice supplies worldwide will need to increase by 1.6% annually to the year 2000 to match population growth estimates. The objectives of this paper are (1) to review the major hypotheses and/or experimental results regarding rice sensitivity to climate change and (2) to evaluate the suitability of existing rice models for assessing the impact of global climate change on rice production. A review of four physiologically-based rice models (RICEMOD, CERES-Rice, MACROS, RICESYS) illustrates their potential to predict rice responses to elevated CO₂ and increased temperature. RICEMOD does not respond to increases in CO₂ nor to large increases in temperature. Both MACROS and CERES (wetland rice) responses to temperature and CO₂ agree with recent experimental data. RICESYS is an ecosystem model which predicts herbivory and inter-species competition between rice and weeds but does not respond to CO₂. Its response to increasing temperature also agrees with experimental data.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, CROP PLANTS, DRY-MATTER PRODUCTION, DYNAMICS, ECOSYSTEMS, PLANT GROWTH, RESPONSES, SIMULATION-MODEL, TEMPERATURE

92

Backhausen, J.E., and R. Scheibe. 1999. Adaptation of tobacco plants to elevated CO₂: influence of leaf age on changes in physiology, redox states and NADP-malate dehydrogenase activity. *Journal of*

Transgenic tobacco plants (*Nicotiana tabacum* L. cv. Xanthi) with altered chloroplast NADP-malate dehydrogenase (NADP-MDH) content were grown under ambient or under doubled atmospheric CO₂ in order to analyse the effect of elevated CO₂ on the redox state of the chloroplasts. Since large differences exist between the individual leaves of tobacco plants, gas exchange characteristics, enzyme capacities and metabolite contents were measured separately for each leaf of the plants. Large variations between leaves of different age were found in nearly every parameter analysed, and the differences between younger and older leaves were, in most cases, larger than the differences between comparable leaves at ambient or elevated CO₂. For all parameters (chlorophyll fluorescence, P700 reduction, NADP-MDH activation) that are indicative for the redox situation in the electron transport chains and in the chloroplast stroma, more oxidized values were determined under elevated CO₂. The increased redox state of ferredoxin, observed at ambient conditions in the NADP-MDH-under-expressing plants, disappeared under elevated CO₂. It was concluded that the reduced rate of photorespiration under elevated CO₂ decreases the amount of excess electrons. Interestingly, this lowered not only the activation state of NADP-MDH, but also the expression of the enzyme in the wild-type plants. The results are discussed with respect to a possible interaction between stromal reduction state and gene expression.

KEYWORDS: ACCLIMATION, CHLOROPHYLL FLUORESCENCE, DEVELOPMENTAL-CHANGES, EXPRESSION, ISOLATED SPINACH-CHLOROPLASTS, LEAVES, PHOTOSYNTHETIC ELECTRON-TRANSPORT, QUANTUM YIELD, SATURATING LIGHT, TRANSCRIPTION FACTOR

93

Badger, M. 1992. Manipulating agricultural plants for a future high CO₂ environment. *Australian Journal of Botany* 40(4-5):421-429.

This paper discusses the potential ways in which C3 plant performance may benefit from a future high-CO₂ environment. These include increases in the efficiencies for light, nitrogen and water utilisation, particularly at elevated temperatures, resulting from the improvement which will occur in the performance of the primary carboxylating enzyme, Rubisco. However, while growth experiments at elevated CO₂ indicate that C3 plants show stimulation of dry matter accumulation, the potential gains are greatly ameliorated by a redistribution of plant resources. This primarily occurs via a reduction in the leaf area ratio which offsets increases in the net assimilation rate. In addition, there may be an overcommitment of nitrogen in key photosynthetic components such as Rubisco and the thylakoid electron transport system. It is concluded that plants may not be genetically adapted to optimise their growth and performance at elevated CO₂ and that consideration should be given to exploring avenues for manipulating plants for more optimal responses. Targets for improvement of growth at elevated CO₂ include (1) altering source-sink relations; (2) improving the redistribution of nitrogen between the photosynthetic machinery and the rest of the plant; and (3) changing the response of stomata to CO₂ and humidity to increase water-use efficiency even further than is currently predicted.

KEYWORDS: ACCLIMATION, C-3, CARBON DIOXIDE, DEPENDENCE, GROWTH, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, TRANSPIRATION

94

Badiani, M., A. Dannibale, A.R. Paolacci, F. Miglietta, and A. Raschi. 1993. The antioxidant status of soybean (*glycine-max*) leaves grown under natural CO₂ enrichment in the field. *Australian Journal of Plant Physiology* 20(3):275-284.

The effects of progressively higher CO₂ levels on the foliar antioxidant status were studied by growing soybean (*Glycine max* Merrill cv. Cresir) plants at decreasing distances from natural CO₂ sources of geothermal origin in central Italy. When compared with neighbouring controls grown under normal CO₂ concentration (C), soybean leaves grown at 2 x C, 7 x C and more than 20 x C showed a substantial reduction in the size of ascorbate pool and in the activity of Cu,Zn-superoxide dismutase; both the content of ascorbic acid and the activity of ascorbate peroxidase declined at 2 x C and 7 x C and recovered to the control values at 20 x C. The foliar titre of glutathione disulfide and the activities of glutathione disulfide reductase and Mn-superoxide dismutase progressively increased as CO₂ concentration increased in ambient air. The results obtained suggest that the immanent risk of dioxygen toxicity associated with photosynthetic electron flow could be reduced in the presence of high CO₂ levels. On the other hand, depending on both the CO₂ exposure regimes and the cell compartment considered, high CO₂ could promote oxidative processes which cause GSH oxidation and require an enhanced cellular ability to scavenge superoxide anion and hydrogen peroxide.

KEYWORDS: ACCUMULATION, EXCESS SULFUR, FLOW, PLANTS, RESPIRATION, TEMPERATURE

95

Badiani, M., A.R. Paolacci, A. Fusari, I. Bettarini, E. Brugnoli, M. Lauteri, F. Miglietta, and A. Raschi. 1998. Foliar antioxidant status of plants from naturally high-CO₂ sites. *Physiologia Plantarum* 104(4):765-771.

We compared the foliar antioxidant status of native *Agrostis stolonifera* L. communities growing at two distinct CO₂-enriched sites of geothermal origin (E) and at a control field location with normal CO₂. Compared to the control, plants from both E- sites showed an increased size of the GSH pool, essentially due to enhanced GSSG levels, and a consequent decrease in the ratio between reduced and oxidised glutathione forms. Such differences were maintained and even enhanced in the vegetatively-propagated progenies of control and E-plants, grown under both greenhouse conditions and normal CO₂ levels. The above results confirmed previous observations on native and crop plants exposed to elevated CO₂. It is therefore suggested that changes in the glutathione redox balance might be of adaptive significance under conditions of permanent exposure to high CO₂.

KEYWORDS: ACTIVE OXYGEN, DETOXIFICATION, DROUGHT STRESS, ELEVATED CO₂, ENZYMES, EXCESS SULFUR, GLUTATHIONE, GLYCINE, LEAVES, PICEA-ABIES

96

Bailey, S., J. Rebbeck, and K.V. Loats. 1999. Interactive effects of elevated ozone plus carbon dioxide on duckweeds exposed in open-top chambers. *Ohio Journal of Science* 99(2):19-25.

The response of *Lemna minor* L. and *Spirodela polyrhiza* (L.) Schleiden to projected future ambient levels of O₃ and CO₂ was studied under field conditions. The two duckweed species were treated with either charcoal-filtered air (CF), ambient O₃ (IXO(3)), or twice ambient O₃ (2XO(3)), twice ambient CO₂ plus twice ambient O₃ (2XCO(2)+2XO(3)), or chamberless open-air (OA). Two experiments were conducted. In Experiment I, *L. minor* was treated for 15 d with a cumulative O₃ exposure of 14.4 ppm.h. No O₃ effects were observed during Experiment I. Dry weight of individual fronds and photosynthesis per frond increased in *L. minor* exposed to 2XCO(2)+2XO(3)(-) air. In Experiment II after 25 d of treatment (cumulative O₃ exposure of 16.2 ppm h), negative effects of 2XO(3) on the photosynthetic and growth rates of *L. minor* were observed. Dark respiration of *L. minor* significantly increased in 2XO(3)-air compared with controls, but

declined significantly in 2XCO(2)+2XO(3)-air compared to those grown in 2XO(3)-air. Photosynthesis and drg weight per frond increased in 2XCO(2)+2XO(3)-air when compared with all other treatments. Measurement of A/C-i (assimilation versus intercellular CO₂ concentration) curves in *L. minor* showed a significant reduction in carboxylation efficiency and maximum rates of photosynthesis in 2XCO(2)+2XO(3)-air compared with other treatments when expressed per weight. No differences in carboxylation efficiency were detected between treatments when expressed per frond. After 25 d of treatment, photosynthesis (per frond) and dry weight of *S. polyrhiza* were reduced in 2XO(3)-air, but final frond number was unaffected. Dark respiration of *S. polyrhiza* was unaffected in 2XO(3)-air, but when exposed to 2XCO(2)+2XO(3)-air, it declined significantly. Although *S. polyrhiza* photosynthesis per frond increased in 2XCO(2)+2XO(3)-air, dry weight was unaffected when compared with all other treatments. Only when comparisons were made between *S. polyrhiza* grown in 2XCO(2)+2XO(3)-air and 2XO(3)-air, were significant increases in dry weight observed. The addition of 2XCO(2) to 2XO(3)-air resulted in amelioration of negative O-3 effects for most responses for both duckweed species.

KEYWORDS: ASPEN CLONES, ATMOSPHERIC CO₂, CO₂ CONCENTRATION, FIELD, GROWTH, O-3, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC RESPONSES, PLANTS, SULFUR-DIOXIDE

97

Baille, M., R. RomeroAranda, and A. Baille. 1996. Gas-exchange responses of rose plants to CO₂ enrichment and light. *Journal of Horticultural Science* 71(6):945-956.

This paper describes the response of gas exchange rates and water use efficiency of rose plants, by means of the characterization in situ and the analysis of the response of photosynthesis, transpiration and water use efficiency of whole plants to CO₂ enrichment under the irradiance conditions prevailing in greenhouses of southern France. Net CO₂ assimilation (A(n)) and transpiration (E) of whole rose plants (*Rosa hybrida*, cv. Sonia) were measured during winter and spring periods. The response of A(n) to light and CO₂ were fitted to a double hyperbola function ($r^2 = 0.84$). Maximum net assimilation rate (A(nmax)), light and CO₂ utilization efficiencies (alpha(1), alpha(c)) as well as light and CO₂ compensation points (Gamma(1), Gamma(c)) were calculated for the whole plant and compared with leaf and canopy data in the literature. The whole-plant characteristics generally had values intermediate between those related to leaf and canopy. Light saturation at subambient air CO₂ concentration (C-a) was reached for relatively low PPFD values (300 mu mol m⁻² s⁻¹), whereas at ambient and enriched C-a light saturation occurs for PPFD approximate to 1000 mu mol m⁻² s⁻¹. Doubling C-a from 350 to 700 mu mol mol⁻¹ increased A(nmax) and alpha(1) by respectively 40% and 30%, while reducing Gamma(1) by 27%. A threefold increase of C-a from 350 to 1050 mu mol mol⁻¹ induced a reduction of 20% of E. Instantaneous transpirational water use efficiency, WUE (=A(n)/E), is relatively insensitive to PPFD, although a slight decrease with PPFD is observed at high CO₂ concentration, but shows marked variations with C-a and leaf to air vapour pressure deficit (D-1). Increase of C-a from 350 to 1000 mu mol mol⁻¹ gave about 50% increase in WUE. Increase of D-1 from 0 to 2 kPa induced 30% decrease in WUE at ambient C-a and 50% decrease at 1000 mu mol mol⁻¹.

KEYWORDS: CARBON DIOXIDE, CROP, LEAF CONDUCTANCE, LEAVES, NET PHOTOSYNTHESIS, PRODUCTIVITY, SWEET-PEPPER, TOMATO, TRANSPIRATION, WATER-USE EFFICIENCY

98

Bainbridge, G., P. Madgwick, S. Parmar, R. Mitchell, M. Paul, J. Pitts, A.J. Keys, and M.A.J. Parry. 1995. Engineering rubisco to

change its catalytic properties. *Journal of Experimental Botany* 46:1269-1276.

The initial steps of carbon assimilation and photorespiration are catalysed by ribulose-1,5-bisphosphate carboxylase/oxygenase (EC 4.1.1.39). Natural variation in the kinetic properties of the enzyme suggest that it is possible to alter the enzyme to favour the carboxylation activity relative to oxygenation. Mutagenesis in vitro of the gene encoding the large subunit of the enzyme from *Anacystis nidulans* has been used to modify catalytic properties. Residues at the C-terminal end of loop 6 of the beta/alpha barrel structure of the large subunit influence specificity towards the gaseous substrates, CO₂ and O-2. None of the residues altered by mutagenesis appear to interact directly with the transition state analogue and their effect on the reaction of the enediolate intermediate with the gaseous substrates and stabilization of the resulting transition state intermediates by lysine 334 must be indirect. Interactions with other parts of the enzyme must also be important in determining substrate specificity. Backbone carbonyl groups close to lysine 334 interact with lysine 128; mutation of lysine 128 to residues of less positive polarity reduces enzyme activity and favours oxygenation relative to carboxylation, the likely effects on assimilation rates of altering the kinetic properties of Rubisco have been modelled. A leaf with cyanobacterial Rubisco may out-perform a higher plant Rubisco at elevated CO₂ and cool temperatures.

KEYWORDS: 1,5-BISPHOSPHATE CARBOXYLASE, ACTIVE-SITE, CO₂/O₂ SPECIFICITY, LARGE SUBUNIT, RHODOSPIRILLUM-RUBRUM, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SITE-DIRECTED MUTAGENESIS, SUBSTRATE-SPECIFICITY

99

Baker, J.T., S.L. Albrecht, D. Pan, L.H. Allen, N.B. Pickering, and K.J. Boote. 1994. Carbon-dioxide and temperature effects on rice (*oryza-sativa* L, CV ir-72). *Soil and Crop Science Society of Florida Proceedings* 53:90-97.

The current increase in atmospheric carbon dioxide concentration ([CO₂]) along with predictions of possible future increases in global air temperatures have stimulated interest in the effects of [CO₂] and temperature on the growth and yield of food crops. This study was conducted to determine the effects and possible interactions of elevated [CO₂] and temperature on the development, growth and yield of rice (*Oryza sativa* L., cv. IR-72). Rice plants were grown season-long in outdoor, naturally sunlit, controlled-environment, plant growth chambers. Chamber air temperatures were controlled to follow a continuously and diurnally varying, near sine-wave control setpoint that operated between maximum (daytime) and minimum (nighttime) values. Day/night (maximum/minimum) air temperature treatments were: 32/23, 35/26, and 38/29-degrees-C. Dewpoint air temperatures were maintained at 18, 21, 24- degrees-C in the 32/23, 35/26, 38/29-degrees-C dry bulb air temperature treatment, respectively. Daytime [CO₂] was controlled to 330 and 660 mumol CO₂ mol⁻¹ air in each of the air temperature treatments. The time interval between appearance of successive mainstem leaves during reproductive development was reduced by increasing air temperature treatment (P less-than-or-equal-to 0.05) but was not affected by [CO₂] enrichment. In this experiment [CO₂] enrichment did not affect (P less-than-or-equal-to 0.10) grain yield, components of grain yield, final above ground biomass or harvest index. Increasing temperature during growth, particularly from the 35/26 to 38/29-degrees-C reduced grain yield, individual grain mass, and harvest index. The reduced grain yields with increasing temperature treatment suggest potential detrimental effects on rice production in some areas if air temperatures increase.

Baker, J.T., and L.H. Allen. 1993. Contrasting crop species responses to CO₂ and temperature - rice, soybean and citrus. *Vegetatio* 104:239-260.

The continuing increase in atmospheric carbon dioxide concentration ([CO₂]) and projections of possible future increases in global air temperatures have stimulated interest in the effects of these climate variables on plants and, in particular, on agriculturally important food crops. Mounting evidence from many different experiments suggests that the magnitude and even direction of crop responses to [CO₂] and temperature is almost certain to be species dependent and very likely, within a species, to be cultivar dependent. Over the last decade, [CO₂] and temperature experiments have been conducted on several crop species in the outdoor, naturally-sunlit, environmentally controlled, plant growth chambers by USDA-ARS and the University of Florida, at Gainesville, Florida, USA. The objectives for this paper are to summarize some of the major findings of these experiments and further to compare and contrast species responses to [CO₂] and temperature for three diverse crop species: rice (*Oryza sativa*, L.), soybean (*Glycine max*, L.) and citrus (various species). Citrus had the lowest growth and photosynthetic rates but under [CO₂] enrichment displayed the greatest percentage increases over ambient [CO₂] control treatments. In all three species the direct effect of [CO₂] enrichment was always an increase in photosynthetic rate. In soybean, photosynthetic rate depended on current [CO₂] regardless of the long-term [CO₂] history of the crop. In rice, photosynthetic rate measured at a common [CO₂], decreased with increasing long-term [CO₂] growth treatment due to a corresponding decline in RuBP carboxylase content and activity. Rice specific respiration decreased from subambient to ambient and superambient [CO₂] due to a decrease in plant tissue nitrogen content and a decline in specific maintenance respiration rate. In all three species, crop water use decreased with [CO₂] enrichment but increased with increases in temperature. For both rice and soybean, [CO₂] enrichment increased growth and grain yield. Rice grain yields declined by roughly 10% per each 1-degree-C rise in day/night temperature above 28/21-degree-C.

KEYWORDS: ATMOSPHERIC CO₂, CANOPY PHOTOSYNTHESIS, CARBON-DIOXIDE CONCENTRATION, CLIMATE SENSITIVITY, DARK RESPIRATION, DEVELOPMENTAL STAGES, ELEVATED CO₂, SHORT- TERM, SOUR ORANGE TREES, WATER-USE EFFICIENCY

101

Baker, J.T., and L.H. Allen. 1994. Assessment of the impact of rising carbon-dioxide and other potential climate changes on vegetation. *Environmental Pollution* 83(1-2):223-235.

The projected doubling of current levels of atmospheric carbon dioxide concentration ([CO₂]) during the next century along with increases in other radiatively active gases have led to predictions of increases in global air temperature and shifts in precipitation patterns. Additionally, stratospheric ozone depletion may result in increased ultraviolet-B (UV-B) radiation incident at the Earth's surface in some areas. Since these changes in the Earth's atmosphere may have profound effects on vegetation, the objectives of this paper are to summarize some of the recent research on plant responses to [CO₂], temperature and UV-B radiation. Elevated [CO₂] increases photosynthesis and usually results in increased biomass, and seed yield. The magnitude of these increases and the specific photosynthetic response depends on the plant species, and are strongly influenced by other environmental factors including temperature, light level, and the availability of water and nutrients. While elevated [CO₂] reduces transpiration and increases photosynthetic water-use efficiency, increasing air temperature can result in greater water use, accelerated plant developmental rate, and shortened growth duration. Experiments on UV-B radiation exposure have demonstrated a wide range of photobiological responses among plants with decreases

in photosynthesis and plant growth among more sensitive species. Although a few studies have addressed the interactive effects of [CO₂] and temperature on plants, information on the effects of UV-B radiation at elevated [CO₂] is scarce. Since [CO₂], temperature and UV-B radiation may increase concurrently, more research is needed to determine plant responses to the interactive effects of these environmental variables.

KEYWORDS: DIFFERENT CO₂ ENVIRONMENTS, DRY-MATTER PRODUCTION, FIELD CONDITIONS, HIGH ATMOSPHERIC CO₂, MILD WATER-STRESS, NET PHOTOSYNTHESIS, PHOTON FLUX-DENSITY, PLANT GROWTH, SOYBEAN CANOPY PHOTOSYNTHESIS, ULTRAVIOLET-B RADIATION

102

Baker, J.T., L.H. Allen, and K.J. Boote. 1990. Growth and yield responses of rice to carbon-dioxide concentration. *Journal of Agricultural Science* 115:313-320.

Rice plants (*Oryza sativa* L., cv. IR30) were grown in paddy culture in outdoor, naturally sunlit, controlled-environment, plant growth chambers at Gainesville, Florida, USA, in 1987. The rice plants were exposed throughout the season to subambient (160 and 250), ambient (330) or superambient (500, 660, 900 $\mu\text{-mol CO}_2/\text{mol air}$) CO₂ concentrations. Total shoot biomass, root biomass, tillering, and final grain yield increased with increasing CO₂ concentration, the greatest increase occurring between the 160 and 500 $\mu\text{-mol CO}_2/\text{mol air}$ treatments. Early in the growing season, root:shoot biomass ratio increased with increasing CO₂ concentration; although the ratio decreased during the growing season, net assimilation rate increased with increasing CO₂ concentration and decreased during the growing season. Differences in biomass and lamina area among CO₂ treatments were largely due to corresponding differences in tillering response. The number of panicles/plant was almost entirely responsible for differences in final grain yield among CO₂ treatments. Doubling the CO₂ concentration from 330 to 660 $\mu\text{-mol CO}_2/\text{mol air}$ resulted in a 32% increase in grain yield. These results suggest that important changes in the growth and yield of rice may be expected in the future as the CO₂ concentration of the earth's atmosphere continues to rise.

KEYWORDS: ATMOSPHERIC CO₂, CENTURIES, CROP PLANTS, DRY-MATTER, ENRICHMENT, ICE CORE, LEAF-AREA, PLANT GROWTH, TEMPERATURE, WHEAT

103

Baker, J.T., L.H. Allen, and K.J. Boote. 1992. Response of rice to carbon-dioxide and temperature. *Agricultural and Forest Meteorology* 60(3-4):153-166.

The current increase in atmospheric carbon dioxide concentration ([CO₂]) along with predictions of possible future increases in global air temperatures have stimulated interest in the effects of [CO₂] and temperature on the growth and yield of food crops. This study was conducted to determine the effects and possible interactions of [CO₂] and temperature on the growth and yield of rice (*Oryza sativa* L., cultivar IR-30). Rice plants were grown for a season in outdoor, naturally sunlit, controlled-environment, and plant growth chambers. Temperature treatments of 28/21/25, 34/27/31, and 40/33/37- degrees-C (daytime dry bulb air temperature/night-time dry bulb air temperature/paddy water temperature) were maintained in [CO₂] treatments of 330 and 660- $\mu\text{-mol CO}_2/\text{mol air}$. In the 40/33/37-degree-C temperature treatment, plants in the 330- $\mu\text{-mol CO}_2/\text{mol air}$ [CO₂] treatment died during stem extension while the [CO₂] enriched plants survived but produced sterile panicles. Plants in the 34/27/31-degree-C temperature treatments accumulated biomass and leaf area at a faster rate early in the growing season than plants in the 28/21/25-degree-C temperature treatments.

Tillering increased with increasing temperature treatment. Grain yield increases owing to [CO₂] enrichment were small and non-significant. This lack of [CO₂] response on grain yield was attributed to the generally lower levels of solar irradiance encountered during the late fall and winter when this experiment was conducted. Grain yields were affected much more strongly by temperature than [CO₂] treatment. Grain yields declined by an average of approximately 7-8% per 1-degree-C rise in temperature from the 28/21/25 to 34/27/31-degree-C temperature treatment. The reduced grain yields with increasing temperature treatment suggests potential detrimental effects on rice production in some areas if air temperatures increase, especially under conditions of low solar irradiance.

KEYWORDS: AIR-TEMPERATURE, CLIMATE SENSITIVITY, CO₂-ENRICHMENT, ENVIRONMENTS, ORYZA SATIVA L, PHOTOSYNTHESIS, PLANT GROWTH, TRANSPIRATION, WHEAT, YIELD

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Baker, J.T., L.H. Allen, and K.J. Boote. 1992. Temperature effects on rice at elevated CO₂ concentration. *Journal of Experimental Botany* 43(252):959-964.

The continuing increase in atmospheric carbon dioxide concentration ([CO₂]) and projections of possible future increases in global air temperatures have stimulated interest in the effects of these climate variables on agriculturally important food crops. This study was conducted to determine the effects of [CO₂] and temperature on rice (*Oryza sativa* L., cv. IR-30). Rice plants were grown season-long in outdoor, naturally sunlit, controlled-environment, plant growth chambers in temperature regimes ranging from 25/18/21-degree-C to 37/30/34-degree-C (daytime dry bulb air temperature/night-time dry bulb air temperature/paddy water temperature) and [CO₂] of 660-mu-mol CO₂ mol⁻¹ air. An ambient chamber was maintained at a [CO₂] of 330-mu-mol mol⁻¹ and temperature regime of 28/21/25-degree-C. Carbon dioxide enrichment at 28/21/25-degree-C increased both biomass accumulation and tillering and increased grain yield by 60%. In the 660-mu-mol mol⁻¹ [CO₂] treatment, grain yield decreased from 10.4 to 1.0 Mg ha⁻¹ with increasing temperature from 28/21/25-degree-C to the 37/30/34-degree-C temperature treatment. Across this temperature range, the number of panicles plant⁻¹ nearly doubled while the number of seeds panicle⁻¹ declined sharply. These results indicate that while future increases in atmospheric [CO₂] are likely to be beneficial to rice growth and yield, potentially large negative effects on rice yield are possible if air temperatures also rise.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CLIMATE SENSITIVITY, ENRICHMENT, GROWTH, ORYZA SATIVA L, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION, WHEAT, YIELD

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Baker, J.T., L.H. Allen, K.J. Boote, and N.B. Pickering. 1997. Rice responses to drought under carbon dioxide enrichment .1. Growth and yield. *Global Change Biology* 3(2):119-128.

Projections of future climate change include a strong likelihood of a doubling of current atmospheric carbon dioxide concentration ([CO₂]) and possible shifts in precipitation patterns. Drought stress is a major environmental limitation for crop growth and yield and is common in rainfed rice production systems. This study was conducted to determine the growth and grain yield responses of rice to drought stress under [CO₂] enrichment. Rice (cv. IR-72) was grown to maturity in eight naturally sunlit, plant growth chambers in atmospheric carbon dioxide concentrations [CO₂] of 350 and 700 mu mol CO₂ mol⁻¹ air. In both [CO₂], water management treatments included continuously hooded (CF) controls, flood water removed and drought stress imposed at

panicle initiation (PI), anthesis (ANT), and both panicle initiation and anthesis (PI & ANT). The [CO₂] enrichment increased growth, panicles plant⁻¹ and grain yield. Drought accelerated leaf senescence, reduced leaf area and above-ground biomass and delayed crop ontogeny. The [CO₂] enrichment allowed 1-2 days more growth during drought stress cycles. Grain yields of the PI and PI & ANT droughts were similar to the CF control treatments while the ANT drought treatment sharply reduced growth, grain yield and individual grain mass. We conclude that in the absence of air temperature increases, future global increases in [CO₂] should promote rice growth and yield while providing a modest reduction of near 10% in water use and so increase drought avoidance.

KEYWORDS: CO₂-ENRICHMENT, CULTIVAR, INCREASE, NUTRITION, ORYZA SATIVA L, WHEAT

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Baker, J.T., L.H. Allen, K.J. Boote, and N.B. Pickering. 1997. Rice responses to drought under carbon dioxide enrichment .2. Photosynthesis and evapotranspiration. *Global Change Biology* 3(2):129-138.

Future climate change is projected to include a strong likelihood of continued increases in atmospheric carbon dioxide concentration ([CO₂]) and possible shifts in precipitation patterns. Due mainly to uncertainties in the timing and amounts of monsoonal rainfall, drought is common in rainfed rice production systems. The objectives of this study were to quantify the effects and possible interactions of [CO₂] and drought stress on rice (*Oryza sativa*, L.) photosynthesis, evapotranspiration and water-use efficiency. Rice (cv. IR-72) was grown to maturity in eight naturally sunlit, plant growth chambers in atmospheric carbon dioxide concentrations [CO₂] of 350 and 700 mu mol CO₂ mol⁻¹ air. In both [CO₂], water management treatments included continuously flooded controls, flood water removed and drought stress imposed at panicle initiation, anthesis, and both panicle initiation and anthesis. Potential acclimation of rice photosynthesis to long-term [CO₂] growth treatments of 350 and 700 mu mol mol⁻¹ was tested by comparing canopy photosynthesis rates across short-term [CO₂] ranging from 160 to 1000 mu mol mol⁻¹. These tests showed essentially no acclimation response with photosynthetic rate being a function of current short-term [CO₂] rather than long-term [CO₂] growth treatment. In both long-term [CO₂] treatments, photosynthetic rate saturated with respect to [CO₂] near 510 mu mol mol⁻¹. Carbon dioxide enrichment significantly increased both canopy net photosynthetic rate (21-27%) and water-use efficiency while reducing evapotranspiration by about 10%. This water saving under [CO₂] enrichment allowed photosynthesis to continue for about one to two days longer during drought in the enriched compared with the ambient [CO₂] control treatments.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CARBOXYLASE, DIFFERENT CO₂ ENVIRONMENTS, DRY-MATTER PRODUCTION, ELEVATED CO₂, PLANT GROWTH, SOYBEAN LEAVES, TEMPERATURE, TRANSPIRATION

107

Balaguer, L., J.D. Barnes, A. Panicucci, and A.M. Borland. 1995. Production and utilization of assimilates in wheat (*Triticum aestivum* L.) leaves exposed to elevated O₃ and/or CO₂. *New Phytologist* 129(4):557-568.

This study examined the effects of elevated ozone (O₃) and/or carbon dioxide (CO₂) on the diel allocation of photosynthetically fixed carbon in fully expanded leaves of young (growth stages 4-5) spring wheat (*Triticum aestivum* L. cv. Hanno). Plants were grown in controlled environment chambers and exposed to two O₃ regimes ['non-polluted' air (CF), < 5 nmol mol⁻¹]; 'polluted' air, CF + 75 nmol mol⁻¹) 7 h d(-

1)] and two CO₂ treatments ('ambient', 354 μmol mol⁻¹; 'elevated', 700 μmol mol⁻¹) over a 30 d period. Neutral sugars (predominantly sucrose) were found to be the most abundant form of carbohydrate accumulated by leaves during the day, but significant quantities of starch and high degree of polymerization (d.p.) fructans were also present. Elevated concentrations of O₃ and/or CO₂ were found to have marked effects on diel patterns of export, storage and respiration, whilst the proportions of fixed carbon allocated to each of these processes were broadly similar. O₃ depressed the rate of net CO₂ assimilation (-20%) and reduced stomatal conductance (-19%). This was reflected in a reduced amount of carbohydrate accumulated in, and exported by, source tissue during the day. Effects of O₃ on the rate of CO₂ fixation were aggravated by an increased demand for carbon by dark respiratory processes. In contrast, doubling the atmospheric concentration of CO₂ enhanced the rate of net CO₂ assimilation (+47%) and reduced the proportion of fixed carbon retained in the leaf blade, increasing the rate of export. The favourable carbon balance of CO₂ enriched leaves was further enhanced by a decrease in the cost of maintenance respiration, whilst simultaneous measurements of CO₂ efflux and O₂ uptake at night suggested a shift in the substrates metabolized at high CO₂. Effects of elevated CO₂ and O₃ on the carbon balance of individual leaf blades over a single 24 h light/dark cycle were entirely consistent with the cumulative effects of the gases on plant growth over a 30 d period. O₃ reduced the rate of plant growth (-10%), but there were differential effects of O₃ on the growth of root and shoot which exacerbated the decrease in assimilate availability induced by O₃. In contrast the favourable effects of CO₂ enrichment on the carbon balance of individual source leaves was reflected in the enhanced accumulation of dry matter in existing sinks, and the initiation of new sinks (i.e. increased tillering). In the combined treatment (elevated CO₂ + O₃), O₃ counteracted the favourable effects of CO₂ enrichment on the carbon balance of individual leaves, and the combined effects of the individual gases on the diel partitioning of photosynthetically fixed carbon in fully expanded leaf blades was reflected in a decreased rate of plant growth at elevated CO₂, a situation further exacerbated by O₃-induced shifts in the relative partitioning of carbon between root and shoot. There was no evidence that CO₂ enrichment afforded additional protection against O₃ damage: the extent of the O₃-induced reduction in photosynthesis, carbohydrate availability and growth observed at elevated CO₂ was similar to that induced by O₃ in ambient air, despite additive effects of the gases on stomatal conductance that would reduce the effective dose of O₃ by approximate to 30%. The wider ecological significance of interactions between elevated CO₂ and O₃ is discussed in the light of other recent findings.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, CLIMATE CHANGE, GAS-EXCHANGE, LEAF BLADES, MAINTENANCE RESPIRATION, OPEN-TOP CHAMBERS, OZONE, PICEA-ABIES L, SOURCE-SINK RELATIONS

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Balaguer, L., E. Manrique, A. de los Rios, C. Ascaso, K. Palmqvist, M. Fordham, and J.D. Barnes. 1999. Long-term responses of the green-algal lichen *Parmelia caperata* to natural CO₂ enrichment. *Oecologia* 119(2):166-174.

Acclimation to elevated CO₂ was investigated in *Parmelia caperata* originating from the vicinity of a natural CO₂ spring, where the average daytime CO₂ concentration was 729 ± 39 μmol mol⁻¹ dry air. Thalli showed no evidence of a down-regulation in photosynthetic capacity following long-term exposure to CO₂ enrichment in the field; carboxylation efficiency, total Ribulose biphosphate carboxylase/oxygenase (Rubisco) content, apparent quantum yield of CO₂ assimilation, and the light-saturated rate of CO₂ assimilation (measured under ambient and saturating CO₂ concentrations) were similar in thalli from the naturally CO₂ enriched site and an adjacent control site where the average long-term CO₂ concentration was about

355 μmol mol⁻¹. Thalli from both CO₂ environments exhibited low CO₂ compensation points and early saturation of CO₂ uptake kinetics in response to increasing external CO₂ concentrations, suggesting the presence of an active carbon-concentrating mechanism. Consistent with the lack of significant effects on photosynthetic metabolism, no changes were found in the nitrogen content of thalli following prolonged exposure to elevated CO₂. Detailed intrathalline analysis revealed a decreased investment of nitrogen in Rubisco in the pyrenoid of algae located in the elongation zone of thalli originating from elevated CO₂, an effect associated with a reduction in the percentage of the cell volume occupied by lipid bodies and starch grains. Although these differences did not affect the photosynthetic capacity of thalli, there was evidence of enhanced limitations to CO₂ assimilation in lichens originating from the CO₂-enriched site. The light-saturated rate of CO₂ assimilation measured at the average growth CO₂ concentration was found to be significantly lower in thalli originating from a CO₂-enriched atmosphere compared with that of thalli originating and measured at ambient CO₂. At lower photosynthetic photon flux densities, the light compensation point of net CO₂ assimilation was significantly higher in thalli originating from elevated CO₂ and this effect was associated with higher usnic acid content.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, CHLOROPHYTA, ELEVATED CO₂, EXCHANGE, GROWTH, PHOTOBIONTS, PHOTOSYNTHESIS, PLANTS, RISING ATMOSPHERIC CO₂, WATER-CONTENT

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Balaguer, L., F. Valladares, C. Ascaso, J.D. Barnes, A. DelosRios, E. Manrique, and E.C. Smith. 1996. Potential effects of rising tropospheric concentrations of CO₂ and O₃ on green-algal lichens. *New Phytologist* 132(4):641-652.

Parmelia sulcata Taylor was used as a model to examine the effects of elevated CO₂ and/or O₃ on green algal lichens. Thalli were exposed for 30 d in duplicate controlled-environment chambers to two atmospheric concentrations of CO₂ ('ambient' [350 μmol mol⁻¹]) and 'elevated' [700 μmol mol⁻¹] 24 h d⁻¹) and two O₃ regimes ('non-polluted' air [CF₂ < 5 nmol mol⁻¹]) and 'polluted' air [15 nmol mol⁻¹] overnight rising to a midday maximum of 75 nmol mol⁻¹), in a factorial design. Elevated CO₂ or elevated O₃ depressed the light saturated rate of CO₂ assimilation (A(sat)) measured at ambient CO₂ by 30%, and 18%, respectively. However, despite this effect ultrastructural studies revealed increased lipid storage in cells of the photobiont in response to CO₂-enrichment. Simultaneous exposure to elevated O₃ reduced CO₂-induced lipid accumulation and reduced A(sat) in an additive manner. Gold-antibody labelling revealed that the decline in photosynthetic capacity induced by elevated CO₂ and/or O₃ was accompanied by a parallel decrease in the concentration of Rubisco in the algal pyrenoid (r = 0.93). Interestingly, differences in the amount of Rubisco protein were not correlated with changes in pyrenoid volume. Measurements of in vivo chlorophyll-fluorescence induction kinetics showed that the decline in A(sat) induced by elevated CO₂ and/or O₃ was not associated with significant changes in the photochemical efficiency of photosystem (PS)II. Although the experimental conditions inevitably imposed some stress on the thalli, revealed a significant decline in the efficiency of PS II photochemistry, and enhanced starch accumulation in the photobiont over the fumigation period, the study shows that the green-algal lichen symbiosis might be influenced by future changes in atmospheric composition. Photosynthetic capacity, measured at ambient CO₂, was found to be reduced after a controlled 30 d exposure to elevated CO₂ and/or O₃ and this effect was associated with a parallel decline in the amount of Rubisco in the pyrenoid of algal chloroplasts.

KEYWORDS: BIPHOSPHATE CARBOXYLASE OXYGENASE, CARBON, CHLORELLA, CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, GROWTH, OZONE, PARMELIA-SULCATA,

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Baldocchi, D. 1994. A comparative-study of mass and energy-exchange rates over a closed C-3 (wheat) and an open C-4 (corn) crop .2. Co₂ exchange and water-use efficiency. *Agricultural and Forest Meteorology* 67(3-4):291-321.

Major differences exist between the photosynthetic and transpiration rates Of C3 and C4 leaves as a result of biochemical and physiological factors. Whether or not differences between CO₂ and water vapor exchange rates Of C3 and C4 species scale from leaf to field dimensions is poorly known. The aim of this work is to improve our understanding on how environmental, architectural and physiological variables affect the flux densities Of CO₂ and water vapor over C3 and C4 crop stands during day and night periods. Experimental data were obtained over a closed wheat and an open com stand using the eddy correlation method. Interpretation of the field measurements is aided by the use of a canopy photosynthesis/evaporation model. The flux density of absorbed photosynthetically active radiation (Q(a)) had a disproportionate influence on CO₂ flux densities measured over a closed C3 and an open C4 crop. Variations in Q(a) explained over 88% of the variance in daytime CO₂ flux densities, F(c). At night, canopy radiative temperature was the main environmental factor controlling the respiratory CO₂ efflux by the two crops. Leaf area index and growth stage were the plant variables that affected F(c) most. Incremental increases in leaf area index enhanced the com crop's ability to absorb incident solar radiation and enlarged the com's sink strength for CO₂. Heading by the wheat caused rates of daytime CO₂ gains to decrease and rates of night-time CO₂ losses to increase. Water use efficiency of the wheat crop improved as the absolute humidity deficit of the atmosphere decreased. Water use efficiency of the com, on the other hand, was relatively insensitive to humidity deficits. With regard to canopy CO₂ exchange and water use efficiency, differences in canopy structure between the wheat and com overwhelmed physiological differences. The closed C3 wheat crop assimilated CO₂ at a higher rate than the sparse C4 com canopy, even though com uses a more efficient photosynthetic pathway. Consequently, water use efficiency of the com was not greater than values measured over the wheat. Instead, water use efficiencies of the two crops were similar. The com crop assimilated CO₂ at a lower rate than wheat because the com's canopy quantum yield was lower and because its sparse canopy absorbed less photosynthetically active radiation than the closed wheat stand.

KEYWORDS: ASSIMILATION, CANOPY, CARBON DIOXIDE, FLUX MEASUREMENTS, LEAF-AREA INDEX, PHOTOSYNTHESIS, SOIL RESPIRATION, STOMATAL CONDUCTANCE, VAPOR, WINTER-WHEAT

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Baldocchi, D.D., and P.C. Harley. 1995. Scaling carbon-dioxide and water-vapor exchange from leaf to canopy in a deciduous forest .2. Model testing and application. *Plant, Cell and Environment* 18(10):1157-1173.

The scaling of CO₂ and water vapour transfer from leaf to canopy dimensions was achieved by integrating mechanistic models for physiological (photosynthesis, stomatal conductance and soil/root and bole respiration) and micrometeorological (radiative transfer, turbulent transfer and surface energy exchanges) processes. The main objectives of this paper are to describe a canopy photosynthesis and evaporation model for a temperate broadleaf forest and to test it against field measurements. The other goal of this paper is to use the validated model to address some contemporary ecological and physiological questions concerning the transfer of carbon and water between forest canopies and the atmosphere. In particular, we examine the role of simple versus

complex radiative transfer models and the effect of environmental (solar radiation and CO₂) and ecophysiological (photosynthetic capacity) variables on canopy-scale carbon and water vapour fluxes.

KEYWORDS: CLIMATE CHANGE, CO₂ CONCENTRATIONS, ELEVATED CO₂, PATTERNS, PHOTOSYNTHESIS, PLANT CANOPIES, SENSIBLE HEAT, STOMATAL CONDUCTANCE, TEMPERATURE, TRANSPIRATION

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Ball, A.S. 1991. Degradation by *Streptomyces viridosporus* t7a of plant-material grown under elevated CO₂ conditions. *Fems Microbiology Letters* 84(2):139-142.

The biodegradability of plant material derived from wheat grown under different concentrations of atmospheric CO₂ was investigated using the lignocarbhydrate solubilising actinomycete, *Streptomyces viridosporus*. Growth of *S. viridosporus* and solubilisation of lignocarbhydrate were highest when wheat grown at ambient CO₂ concentrations (350 ppm) was used as C-source. Growth of *S. viridosporus* and solubilisation were reduced when the plant material was derived from wheat grown at 645 PPM CO₂. The results suggest that modifications in plant structure occur when wheat is grown under conditions of elevated atmospheric CO₂ which make it more resistant to microbial digestion.

KEYWORDS: ENZYME, LIGNIN DEGRADATION, LIGNOCELLULOSE, POLYMERIC LIGNIN, STRAW

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Ball, A.S. 1997. Microbial decomposition at elevated CO₂ levels: effect of litter quality. *Global Change Biology* 3(4):379-386.

The decomposition of senesced plant litter represents an important intermediate step in the cycling of nutrients between above-and below-ground systems. The rate of decomposition of plant litter is sensitive to fluctuations in a number of parameters, including environmental conditions, and particularly to changes in the quality of the litter. Increased C:N ratios of litter are thought to be one possible consequence of growth of plants under elevated [CO₂]. This response is likely to reduce the rate of decomposition of the litter. Evidence from the growth of plants in both pot and field studies suggests that growth of C3 plants in elevated atmospheric [CO₂] (600-700 $\mu\text{mol mol}^{-1}$) may lead to a significant increase in either/both the C:N and the lignin: N ratios of litter. Short-term decomposition of litter from plants showing this response in elevated [CO₂] has confirmed that decomposition occurs at a significantly lower rate. The limited studies of both the response of C4 plants to elevated [CO₂] and the subsequent degradability of the senescent litter suggest that no differences in litter quality or degradability occur. In terms of litter quality the response of plants therefore appears to be dependent upon photosynthetic type; the C:N and lignin:N ratios of litter from C3 plants exposed to elevated [CO₂] are increased, leading to lower degradation rates, while the nutrient ratios and degradation rates of litter from C4 plants grown in elevated [CO₂] remain unchanged. To date, very few ecosystem studies of decomposition have been carried out. Further work is required at the ecosystem level to determine whether the effects observed in laboratory, pot and field studies are also observed in long-term, complex ecosystem studies. Clearly if these results are repeated at the ecosystem level then significant changes in the cycling of C and N in important terrestrial ecosystems may occur as a results of elevated [CO₂].

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, ECOSYSTEMS, HARDWOOD LEAF LITTER, LIGNIN CONTENT, MASS-LOSS, NITROGEN DYNAMICS, PLANT-MATERIAL, RESPONSES, SOIL

114

Ball, A.S., and B.G. Drake. 1997. Short-term decomposition of litter produced by plants grown in ambient and elevated atmospheric CO₂ concentrations. *Global Change Biology* 3(1):29-35.

The effects of elevated atmospheric CO₂ (ambient + 340 $\mu\text{mol mol}^{-1}$) on above-ground litter decomposition were investigated over a 6-week period using a field-based mesocosm system. Soil respiratory activity in mesocosms incubated in ambient and elevated atmospheric CO₂ concentrations were not significantly different (t-test, $P > 0.05$) indicating that there were no direct effects of elevated atmospheric CO₂ on litter decomposition. A study of the indirect effects of CO₂ on soil respiration showed that soil mesocosms to which naturally senescent plant litter had been added (0.5% w/w) from the C-3 sedge *Scirpus olneyi* grown in elevated atmospheric CO₂ was reduced by an average of 17% throughout the study when compared to soil mesocosms to which litter from *Scirpus olneyi* grown in ambient conditions had been added. In contrast, similar experiments using senescent material from the C-4 grass *Spartina patens* showed no difference in soil respiration rates between mesocosms to which litter from plants grown in elevated or ambient CO₂ conditions had been added. Analysis of the C:N ratio and lignin content of the senescent material showed that, while the C:N ratio and lignin content of the *Spartina patens* litter did not vary with atmospheric CO₂ conditions, the C:N ratio (but not the lignin content) of the litter from *Scirpus olneyi* was significantly greater (t-test; $P < 0.05$) when derived from plants grown under elevated CO₂ (105:1 compared to 86:1 for litter derived from *Scirpus olneyi* grown under ambient conditions). The results suggest that the increased C:N ratio of the litter from the C-3 plant *Scirpus olneyi* grown under elevated CO₂ led to the lower rates of biodegradation observed as reduced soil respiration in the mesocosms. Further longterm experiments are now required to determine the effects of elevated CO₂ on C partitioning in terrestrial ecosystems.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, DYNAMICS, FORESTS, INSITU, LEAF LITTER, LEAVES, NITROGEN, RESPIRATION, SOIL

115

Ball, A.S., and B.G. Drake. 1998. Stimulation of soil respiration by carbon dioxide enrichment of marsh vegetation. *Soil Biology and Biochemistry* 30(8-9):1203-1205.

KEYWORDS: ELEVATED ATMOSPHERIC CO₂, INSITU, NITROGEN, PLANTS

116

Ball, M.C., M.J. Cochrane, and H.M. Rawson. 1997. Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO₂. *Plant, Cell and Environment* 20(9):1158-1166.

Two mangrove species, *Rhizophora apiculata* and *R. stylosa*, were grown for 14 weeks in a multifactorial combination of salinity (125 and 350 mol m^{-3} NaCl), humidity (43 and 86% relative humidity at 30 degrees C) and atmospheric CO₂ concentration (340 and 700 $\text{cm}^3 \text{m}^{-3}$). Under ambient [CO₂], growth responses to different combinations of salinity and humidity were consistent with interspecific differences in distribution along natural gradients of salinity and aridity in northern Australia. Elevated [CO₂] had little effect on relative growth rate when it was limited by salinity but stimulated growth when limited by humidity. Both species benefited most from elevated [CO₂] under relatively low salinity conditions in which growth was vigorous, but relative growth rate was enhanced more in the less salt-tolerant and more rapidly growing species, *R. apiculata*. Changes in both net assimilation

rate and leaf area ratio contributed to changes in relative growth rates under elevated [CO₂], with leaf area ratio increasing with decrease in humidity. Increase in water use efficiency under elevated [CO₂] occurred with increase, decrease or no change in evaporation rates; water use characteristics which depended on both the species and the growth conditions. In summary, elevated [CO₂] is unlikely to increase salt tolerance, but could alter competitive rankings of species along salinity x aridity gradients.

KEYWORDS: AUSTRALIA, AVICENNIA-MARINA, CARBON DIOXIDE, COTTON, ENRICHMENT, GAS-EXCHANGE, MANGLE L, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, RED MANGROVE

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Ball, M.C., and R. Munns. 1992. Plant-responses to salinity under elevated atmospheric concentrations of CO₂. *Australian Journal of Botany* 40(4-5):515-525.

This review explores effects of elevated CO₂ concentrations on growth in relation to water use and salt balance of halophytic and non-halophytic species. Under saline conditions, the uptake and distribution of sodium and chloride must be regulated to protect sensitive metabolic sites from salt toxicity. Salt-tolerant species exclude most of the salt from the transpiration stream, but the salt flux from a highly saline soil is still considerable. To maintain internal ion concentrations within physiologically acceptable levels, the salt influx to leaves must match the capacities of leaves for salt storage and/or salt export by either retranslocation or secretion from glands. Hence the balance between carbon gain and the expenditure of water in association with salt uptake is critical to leaf longevity under saline conditions. Indeed, one of the striking features of halophytic vegetation, such as mangroves, is the maintenance of high water use efficiencies coupled with relatively low rates of water loss and growth. These low evaporation rates are further reduced under elevated CO₂ conditions. This, with increased growth, leads to even higher water use efficiency. Leaves of plants grown under elevated CO₂ conditions might be expected to contain lower salt concentrations than those grown under ambient CO₂ if salt uptake is coupled with water uptake. However, salt concentrations in shoot tissues are similar in plants grown under ambient and elevated CO₂ conditions despite major differences in water use efficiency. This phenomenon occurs in C3 halophytes and in both C3 and C4 non-halophytes. These results imply shoot/root communication in regulation of the salt balance to adjust to environmental factors affecting the availability of water and ions at the roots (salinity) and those affecting carbon gain in relation to water loss at the leaves (atmospheric concentrations of water vapour and carbon dioxide).

KEYWORDS: AUSTRALIAN MANGROVE FOREST, AVICENNIA-MARINA, BARLEY, CARBON DIOXIDE, DROUGHT, GAS-EXCHANGE, GROWTH, LIMITATIONS, OSMOTIC ADJUSTMENT, PHOTOSYNTHESIS

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Bandara, D.C., H. Nobuyasu, K.G. Ofofu-Budu, T. Ando, and K. Fujita. 1998. Effect of CO₂ enrichment on biomass production, photosynthesis, and sink activity in soybean cv. Bragg and its supernodulating mutant nts 1007. *Soil Science and Plant Nutrition* 44(2):179-186.

Soybean (*Glycine max* L. Merr.) cv. Bragg and its supernodulating mutant nts 1007 were grown in pots containing vermiculite with a N-free nutrient solution in order to examine the effect of elevated CO₂ concentration (100+20 Pa CO₂) on biomass production, photosynthesis, and biological nitrogen fixation. The whole plant weight increase in Bragg was higher than in the mutant at a high CO₂ concentration.

Apparent photosynthetic activities of the upper leaves in both Bragg and the mutant increased up to 14 d after treatment initiation by the CO₂ enrichment and thereafter decreased to some extent. Both leaf area and leaf thickness of Bragg increased more than in nts 1007. With the elevated CO₂ concentration, biological nitrogen fixation (BNF) also responded in the same manner as biomass production in both Bragg and nts 1007. The increase of BNF in Bragg was largely due to an increase in nodule weight. Starch contents in the leaves of both Bragg and the mutant increased significantly by CO₂ enrichment, with a higher increase in Bragg than in its mutant. Sugar content in leaf differed only slightly in both Bragg and the mutant. N content in leaf decreased in both Bragg and its mutant, with the decrease being more pronounced in Bragg. However, in other plant parts (roots, stem, and petiole + pods), N content increased in the mutant while in Bragg, it decreased in the pod. N accumulation rate was higher in Bragg than in the mutant and increased more in Bragg than in the mutant by CO₂ enrichment. The ureide content in leaf decreased in Bragg but increased in the mutant by elevated CO₂ concentration. In the nodules, ureide content increased in both Bragg and the mutant by CO₂ enrichment. Based on these results, it is suggested that in terms of biomass production and photosynthetic rate, Bragg responded more to elevated CO₂ concentration than its mutant nts 1007. The alleviation of the stunted vegetative growth of the mutant by CO₂ enrichment was limited despite the significant increase in the photosynthetic activity, presumably due to the limitation of sink activity in the growing parts and not to insufficient supply of N through BNF.

KEYWORDS: CARBON, DINITROGEN FIXATION, GROWTH, L MERRILL MUTANTS, LEGUMES, NITRATE APPLICATION, NITROGEN, NTS1007, PLANTS, ROOTS

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Barnes, J.D., J.H. Ollerenshaw, and C.P. Whitfield. 1995. Effects of elevated CO₂ and/or O₃ on growth, development and physiology of wheat (*Triticum aestivum* L). *Global Change Biology* 1(2):129-142.

Two cultivars of spring wheat (*Triticum aestivum* L. cvs. Alexandria and Hanno) and three cultivars of winter wheat (cvs. Riband, Mercia and Haven) were grown at two concentrations of CO₂ [ambient (355 μmol mol⁻¹) and elevated (708 μmol mol⁻¹)] under two O₃ regimes [clean air (<5 nmol mol⁻¹) O₃ and polluted air (15 nmol mol⁻¹) O₃ at night rising to a midday maximum of 75 nmol mol⁻¹)] in a phytotron at the University of Newcastle-upon-Tyne. Between the two-leaf stage and anthesis, measurements of leaf gas-exchange, non-structural carbohydrate content, visible O₃ damage, growth, dry matter partitioning, yield components and root development were made in order to examine responses to elevated CO₂ and/or O₃. Growth at elevated CO₂ resulted in a sustained increase in the rate of CO₂ assimilation, but after roughly 6 weeks' exposure there was evidence of a slight decline in the photosynthetic rate (c.-15%) measured under growth conditions which was most pronounced in the winter cultivars. Enhanced rates of CO₂ assimilation were accompanied by a decrease in stomatal conductance which improved the instantaneous water use efficiency of individual leaves. CO₂ enrichment stimulated shoot and root growth to an equivalent extent, and increased tillering and yield components, however, non-structural carbohydrates still accumulated in source leaves. In contrast, long-term exposure to O₃ resulted in a decreased CO₂ assimilation rate (c.-13%), partial stomatal closure, and the accumulation of fructan and starch in leaves in the light. These effects were manifested in decreased rates of shoot and root growth, with root growth more severely affected than shoot growth. In the combined treatment growth of O₃-treated plants was enhanced by elevated CO₂, but there was little evidence that CO₂ enrichment afforded additional protection against O₃ damage. The reduction in growth induced by O₃ at elevated CO₂ was similar to that induced by O₃ at ambient CO₂ despite additive effects of the individual gases on stomatal conductance that would be expected to reduce the O₃ flux by 20%, and also CO₂-

induced increases in the provision of substrates for detoxification and repair processes. These observations suggest that CO₂ enrichment may render plants more susceptible to O₃ damage at the cellular level. Possible mechanisms are discussed.

KEYWORDS: AIR- POLLUTANTS, ATMOSPHERIC CARBON-DIOXIDE, CARBOXYLASE-OXYGENASE, GAS-EXCHANGE, MODERN GREEK CULTIVARS, PICEA-ABIES L, PLANT GROWTH, SOURCE-SINK RELATIONS, SPRING WHEAT, WINTER-WHEAT

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Barnes, J.D., and T. Pfirrmann. 1992. The influence of CO₂ and O₃, singly and in combination, on gas-exchange, growth and nutrient status of radish (*Raphanus sativus* L). *New Phytologist* 121(3):403-412.

Five days after emergence radish (*Raphanus sativus* L. cv. Cherry Belle) plants were transferred to a phytotron at the GSF Munchen, where they were exposed in four large controlled climate chambers to two at atmospheric concentrations of CO₂ ('ambient', daily means of almost-equal-to 385-μmol mol⁻¹; elevated, daily means of almost-equal-to 765-μmol mol⁻¹) and two O₃ regimes ('non-polluted' air, 24 h mean of 20 nmol mol⁻¹; polluted air, 24 h mean of 73 nmol mol⁻¹) Leaf gas-exchange measurements were made at intervals, and visible O₃ damage, effects on growth, dry matter partitioning and mineral composition were assessed at a final whole-plant harvest after 27 d. In 'non-polluted air' CO₂ enrichment resulted in a progressive stimulation in A(sat), whilst there was a decline in g(s) which decreased E (i.e. improved WUE(i)). The extra carbon fixed in elevated CO₂ stimulated growth of the root (+ hypocotyl) by 43 %, but there was no significant effect on shoot growth or leaf area. Moreover, a decline in SLA and LAR in CO₂-enriched plants suggested that less dry matter was invested in leaf area expansion. Tissue concentrations of N, S, P, Mg and Ca were lower (particularly in the root + hypocotyl) in elevated CO₂, indicating that total uptake of these nutrients was not affected by CO₂, and there was an increase in the C:N ratio in root (+ hypocotyl) tissue. In contrast, O₃ depressed A(sat), (almost-equal-to 26 %) and induced slight stomatal closure, with the result that WUE(i) declined. All plants exposed to 'polluted' air developed typical visible symptoms of O₃ injury, and effects on carbon assimilation were reflected in reduced growth, with shoot growth maintained at the expense of the root. In addition, O₃ increased the P and K concentration in shoot and root (+hypocotyl) tissue, indicating enhanced uptake of these nutrients from the growth medium. However, there was no effect of O₃ on tissue concentrations of N, S, Mg and Ca. Interactions between the gases were complex, and often subtle. In general, elevated CO₂ counteracted (at least in part) the detrimental effects of phytotoxic concentrations of O₃, whilst conversely, O₃ reduced the impact of elevated CO₂. Moreover, there were indications that cumulative changes in source:sink relations in O₃-exposed plants may limit plant response to CO₂-enrichment to an even greater extent in the long-term. The future ecological significance of interactions between CO₂ and O₃ are discussed.

KEYWORDS: ABIES L KARST, ACID MIST, AIR- POLLUTANTS, CARBON DIOXIDE, ENRICHMENT, OZONE ALTERS, PHOTOSYNTHESIS, PLANTS, USE EFFICIENCY, WHEAT

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Barnes, J.D., T. Pfirrmann, K. Steiner, C. Lutz, U. Busch, H. Kuchenhoff, and H.D. Payer. 1995. Effects of elevated CO₂, elevated O₃ and potassium deficiency on Norway spruce [*Picea abies* (L.) Karst]: Seasonal changes in photosynthesis and non-structural carbohydrate content. *Plant, Cell and Environment* 18(12):1345-1357.

Two clones of 5-year-old Norway spruce [*Picea abies* (L.) Karst.] were exposed to two atmospheric concentrations of CO₂ (350 and 750 μmol mol⁻¹) and O₃ (20 and 75 nmol mol⁻¹) in a phytotron at the

GSF-Forschungszentrum (Munich) over the course of a single season (April to October), The phytotron was programmed to recreate an artificial climate similar to that at a high elevation site in the Inner Bavarian Forest, and trees were grown in Large containers of forest soil fertilized to achieve contrasting levels of potassium nutrition, designated well-fertilized or K-deficient. Measurements of the rate of net CO₂ assimilation were made on individual needle year age classes over the course of the season, chlorophyll fluorescence kinetics were recorded after approximately 23 weeks, and seasonal changes in non-structural carbohydrate composition of the current year's foliage were monitored. Ozone was found to have contrasting effects on the rate of net CO₂ assimilation in different needle age classes. After c. 5 months of fumigation, elevated O-3 increased (by 33%) the rate of photosynthesis in the current year's needles. However, O-3 depressed (by 30%) the photosynthetic rate of the previous year's needles throughout the period of exposure. Chlorophyll fluorescence measurements indicated that changes in photosystem II electron transport played no significant role in the effects of O-3 on photosynthesis. The reasons for the contrasting effects of O-3 on needles of different ages are discussed in the light of other recent findings. Although O-3 enhanced the rate at which CO₂ was fixed in the current year's foliage, this was not reflected in increases in the non-structural carbohydrate content of the needles. The transfer of ambient CO₂-grown trees to a CO₂-enriched atmosphere resulted in marked stimulation in the photosynthetic rate of current and previous year's foliage. However, following expansion of the current year's growth, the photosynthetic rate of the previous year's foliage declined. The extent of photosynthetic adjustment in response to prolonged exposure to elevated CO₂ depended upon the clone, providing evidence of intraspecific variation in the long-term response of photosynthesis to elevated CO₂. The increase in photosynthesis induced by CO₂ enrichment was associated with increased foliar concentrations of glucose, fructose and starch (but no change in sucrose) in the new growth. CO₂ enrichment significantly enhanced the photosynthetic rate of K-deficient needles, but there was a strong CO₂*soil interaction in the current year's needles, indicating that the long-term response of trees to a high CO₂ environment may depend on soil fertility. Although the rate of photosynthesis and non-structural carbohydrate content of the new needles were increased in O-3-treated plants grown at higher levels of CO₂, there was no evidence that elevated CO₂ provided additional protection against O-3 damage. Simultaneous exposure to elevated O-3 modified the effects of elevated CO₂ on needle photosynthesis and non-structural carbohydrate content, emphasizing the need to take into account not only soil nutrient status but also the impact of concurrent increases in photochemical oxidant pollution in any serious consideration of the effects of climate change on plant production.

KEYWORDS: ACID MIST, AIR-POLLUTANTS, ATMOSPHERIC CO₂, CARBON DIOXIDE, GAS-EXCHANGE, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NONSTOMATAL LIMITATION, OPEN-TOP CHAMBERS, STOMATAL CONDUCTANCE

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Barr, A.G., K.M. King, G.W. Thurtell, and M.E.D. Graham. 1990. Humidity and soil-water influence the transpiration response of maize to CO₂ enrichment. *Canadian Journal of Plant Science* 70(4):941-948.

123

Barrett, D.J., and R.M. Gifford. 1995. Acclimation of photosynthesis and growth by cotton to elevated CO₂: Interactions with severe phosphate deficiency and restricted rooting volume. *Australian Journal of Plant Physiology* 22(6):955-963.

Acclimation of photosynthesis and growth at three CO₂ concentrations (376, 652 and 935 $\mu\text{mol mol}^{-1}$) was examined in cotton grown under three growth-limiting phosphate (P) supplies (2.1, 6.1 and 18.2

mg P plant⁻¹) and where biomass allocation between roots and shoots was altered by pots of three different sizes (0.32 X 10⁻³, 0.72 X 10⁻³ and 1.56 X 10⁻³ m³ pot⁻¹). Phosphate supplies were chosen such that carbon gain at ambient CO₂ increased linearly with P supply. Relative growth rates of these plants were 5-10-times less and photosynthetic rates 3-16-times less than for cotton supplied with abundant nutrients. Pot sizes were chosen so that root biomass and root:shoot ratios decreased with a decrease in rooting volume. Maximum carboxylation rates per unit leaf area (V-cmax) were lower in leaves grown at two elevated CO₂ concentrations, compared with ambient CO₂ concentrations, under all P and pot size treatments indicating that acclimation of photosynthesis had occurred. The degree of photosynthetic acclimation to elevated CO₂ was not related to the degree by which whole plant carbon gain was stimulated by elevated CO₂ concentration at the different P supplies, or to the degree by which allocation to root and shoots was altered by pot size. Thus there is no simple relationship between photosynthetic and growth acclimation by cotton to elevated CO₂. At ambient CO₂, the maximum carboxylation rate increased linearly with an increase in leaf P per unit area (mg P m⁻²), but rates were lower at elevated CO₂ for a given P content m⁻². V-cmax also increased linearly with an increase in leaf P concentration (mg P g⁻¹ structural dry weight). However, values of V-cmax were similar for plants grown at ambient and elevated CO₂, for a given P concentration. Acclimation of photosynthesis at elevated CO₂ was associated with an increase in leaf starch determined 5 h into the light period. However, increased starch concentration with an increase in P supply was not associated with any decline in V-cmax.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, GLYCINE-MAX, LEAVES, LONG-TERM EXPOSURE, NITROGEN, PHOSPHORUS-NUTRITION, PLANTS, RESPONSES

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Barrett, D.J., and R.M. Gifford. 1995. Photosynthetic acclimation to elevated CO₂ in relation to biomass allocation in cotton. *Journal of Biogeography* 22(2-3):331-339.

Biomass allocation to leaf tissues and photosynthetic acclimation to CO₂ by cotton were investigated in two experiments. Plants were grown at ambient and elevated CO₂ concentrations with growth restricting phosphorus supplies in both experiments and in root restricting pot volumes in the first experiment. In both experiments, elevated CO₂ concentrations decreased the maximum carboxylation rate (V-cmax) and the CO₂ saturated rate of photosynthesis indicative of photosynthetic acclimation to elevated CO₂ concentrations. In the first experiment, the percentage reduction in V-cmax under elevated CO₂ concentration was least at a P supply of 2.1 mg P plant⁻¹, greatest at 6.1 mg P plant⁻¹, but then decreased at 18.2 mg P plant⁻¹. The greater acclimation at the middle P supply was associated with a higher ratio of leaf mass to plant mass (LMR) than in other treatments and the lesser acclimation at the highest P treatment coincided with a lower LMR. In the second experiment the reduction in V-cmax at elevated CO₂ was less than in the first experiment but was also associated with a greater allocation of dry matter to leaf tissues during growth. In both experiments, V-cmax was not correlated to the relative degree of biomass enhancement at elevated CO₂ nor with the degree of root growth restriction in small pots. These data support the hypothesis that acclimation of photosynthesis to elevated CO₂ concentrations is mediated by shifts in allocation between leaves and the rest of the plant, induced by environmental conditions during growth, such that carbohydrate supply remains in balance with the utilization capacity of sink tissues.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, LIMITATIONS, PLANTS, SOURCE-SINK RELATIONS

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Barrett, D.J., and R.M. Gifford. 1999. Increased C-gain by an endemic Australian pasture grass at elevated atmospheric CO₂ concentration when supplied with non-labile inorganic phosphorus. *Australian Journal of Plant Physiology* 26(5):443-451.

Limited phosphorus (P) availability in Australia's highly weathered soils may constrain an increase in terrestrial net primary productivity (NPP) with the globally increasing atmospheric CO₂ concentration. We examined whether an Australian temperate pasture grass (*Danthonia richardsonii*) grown in sand culture and supplied solely with virtually insoluble Al- and Fe-phosphate was able to increase C-gain when exposed to elevated (731 $\mu\text{mol mol}^{-1}$) compared with ambient (379 $\mu\text{mol mol}^{-1}$) CO₂ concentrations. When supplied with 8 mg kg⁻¹ insoluble P concentration, total citrate efflux by root systems ($\mu\text{mol h}^{-1}$), plant P uptake, shoot photosynthesis rates and plant mass were all significantly greater at elevated than at ambient CO₂ after a growth period of between 55 and 63 days. In this treatment, although the P concentration of the rooting medium limited growth at ambient CO₂, elevated CO₂ increased P-uptake from the non-labile source, increased photosynthesis rates per unit shoot soluble-P and increased plant mass. At P concentrations lower than 8 mg kg⁻¹, plant mass, specific citrate efflux and maximum leaf carboxylation rates were limited by the amount of P available in the rooting medium and no CO₂ effect was observed. In all treatments, carbon supply did not appear to limit citrate efflux. Where an increase in P uptake at elevated CO₂ was achieved, it was due to an increase in root mass (indicative of a potentially larger soil volume explored) rather than to increased specific rates of citrate efflux. Above 8 mg kg⁻¹, the supplied P concentration was sufficient that minimal rates of specific citrate efflux alone solubilised enough P for growth and a strong CO₂ effect on plant mass, photosynthesis and P uptake was observed.

KEYWORDS: ACCLIMATION, GROWTH, LIMITATIONS, LUPINUS-ALBUS, ORGANIC-ACIDS, PHOSPHATE, PHOTOSYNTHESIS, PROTEOID ROOTS, ROOT EXUDATION, SOLUBILIZATION

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Barrett, D.J., A.E. Richardson, and R.M. Gifford. 1998. Elevated atmospheric CO₂ concentrations increase wheat root phosphatase activity when growth is limited by phosphorus. *Australian Journal of Plant Physiology* 25(1):87-93.

Wheat seedlings were grown in solution culture under adequate and limited phosphorus treatments at current ambient and elevated (approximately 2X ambient) CO₂ concentrations. Acid phosphomonoesterase ('phosphatase') activity of root segments was measured using p-nitrophenyl phosphate as substrate. When plant growth was P-limited, elevated CO₂ concentrations increased phosphatase activity more than at ambient CO₂. This result (1) was evident when expressed on a unit root dry weight or root length basis, indicating that increased root enzyme activity was unlikely to be associated with CO₂-induced changes in root morphology; (2) occurred when plants were grown aseptically, indicating that the increase in phosphatase activity originated from root cells rather than root-associated microorganisms; (3) was associated with shoot P concentrations below 0.18%; (4) occurred only when wheat roots were grown under P deficiency but not when a transient P deficiency was imposed; and (5) suggest that a previously reported increase in phosphatase activity at elevated CO₂ by an Australian native pasture grass (Gifford, Lutze and Barrett 1996; *Plant and Soil* 187, 369-387) was also a root mediated response. The observed increase in phosphatase activity by plant roots at elevated CO₂, if confirmed for a wide range of field pasture and crop species, is one factor which may increase mineralisation of soil organic P as the anthropogenic increase of atmospheric CO₂ concentrations continues. But, whether a concomitant increase in plant uptake of P occurs will depend on the relative influence

of root and microbial phosphatases, and soil geochemistry in determining the rate of mineralisation of soil organic P for any given soil.

KEYWORDS: ACCLIMATION, BIOMASS, CARBON DIOXIDE, DEFICIENCY, EFFICIENCY, ENRICHMENT, ORGANIC PHOSPHORUS, PHOTOSYNTHESIS, PLANT-ROOTS, SOIL

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Bartak, M., I. Nijs, and I. Impens. 1996. The effect of long-term exposure of *Lolium perenne* L plants to elevated CO₂ and/or elevated air temperature on quantum yield of photosystem 2 and net photosynthesis. *Photosynthetica* 32(4):549-562.

The effects of long-term exposure of *Lolium perenne* L. plants to CO₂ concentration elevated to 700 $\mu\text{mol (CO}_2\text{) mol}^{-1}$ (EC) and air temperature elevated by 4 degrees C (ET) on the quantum yield of electron transport of photosystem 2, PS2 ($\phi(2)$) and on the potential yield of photochemical reactions of PS2 (F-v/F-m) measured by the chlorophyll (Chl) fluorescence method, were studied. The plants were exposed for 6 months in opened field greenhouses to four treatments simulating global atmospheric changes: (1) ambient CO₂ (AC) and ambient air temperature, AT (ACAT - control), (2) EC and AT (ECAT), (3) AC and ET (ACET), and (4) EC and ET (ECET). When the plants were exposed to stepwise increased irradiance, a decrease in $\phi(2)$ was found under both AC and EC measuring concentrations. At high irradiances a significantly higher yield of PS2 was detected when measured under EC compared to AC regardless of long-term CO₂ and temperature treatment (i.e., positive short-term effect of EC). The short-term effect of EC on $\phi(2)$ as related to net photosynthetic rate (P-N) Shift was detected from irradiance response curves. At high irradiances and AC, $\phi(2)$ was reduced in comparison to control for the plants of EC and ET treatments (i.e., negative long-term effect of treatment). The long-term effect of both EC and ET on the yield of PS2 was attributed to a down-regulation of P-N caused by the treatment. The $\phi(2)$ was related to the actual rate of photosynthesis and the relationship between $\phi(2)$ and $\phi(\text{CO}_2)$ was linear over a wide range of irradiances. No effect of long-term treatments on the dark-adapted F-v/F-m ratio was found in plants cultivated under natural greenhouse irradiance.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DEPENDENCE, ELECTRON-TRANSPORT, FLOW, GROWTH, LEAVES, LIGHT, REDUCTION, RESPONSES, RISING CO₂

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Bartak, M., I. Nijs, and I. Impens. 1998. The susceptibility of PS II of *Lolium perenne* to a sudden fall in air temperature - response of plants grown in elevated CO₂ and/or increased air temperature. *Environmental and Experimental Botany* 39(1):85-95.

The effect of a sudden fall in air temperature from 20 to 5 degrees C on fast kinetics of chlorophyll fluorescence, maximum yield of the photosystem II photochemical reactions (Fv/Fm), quantum yield of the photosystem II electron transport ($\Phi(\text{II})$) coefficients of photochemical (qP), non-photochemical quenching (qN) was studied in *Lolium perenne* using a modulated chlorophyll fluorescence technique. Before fluorescence measurement, the plants were cultivated in the treatments simulating the likely future climate characterized with elevated air temperature and CO₂ concentration and combination of both. On fast kinetics curves the risetimes of the I and D points characterizing the redox state of Q(A) were affected by lowering the air temperature. At 5 degrees C both the I and D points were reached later than at 20 degrees C. Also the I to D risetime was prolonged at 5 degrees C and it was found significantly longer in plants cultivated in ambient + 4 degrees C temperature. While a significant difference was found in the area over the rising part of the fluorescence curve between 20 and 5 degrees C, no

difference was found in area over the relaxation curve part. Lowering of air temperature to 5 degrees C had no effect on Fv/Fm values in control plants and in the plants cultivated in elevated CO₂ but brought significant decrease in plants cultivated in the ambient + 4 degrees C air temperature. Both Phi(II) and qP decreased with the temperature lowered to 5 degrees C while the values of qN increased. The changes in fluorescence parameters indicated altered functioning of PS II at low temperature. The changes in parameters are discussed as a consequence of decreased enzymatic activity, decreased turnover of plastoquinone pool and photoinhibition. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON DIOXIDE, CENTERS, CHLOROPHYLL FLUORESCENCE, LEAVES, PHOTOINHIBITION, PHOTOSYNTHESIS, PHOTOSYSTEM, QUANTUM YIELD, SENSITIVITY, VIOLAXANTHIN DEEPOXIDATION

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Barton, C.V.M., and P.G. Jarvis. 1999. Growth response of branches of *Picea sitchensis* to four years exposure to elevated atmospheric carbon dioxide concentration. *New Phytologist* 144(2):233-243.

Branch bags were used to expose branches on mature Sitka spruce trees to either ambient [CO₂] (A) or elevated [CO₂] (E) for 4 yr. This paper reports the effects of this treatment on the growth, development and phenology of the branches, including shoot expansion, shoot numbers, needle dimensions, needle numbers and stomatal density. The effect of elevated [CO₂] on the relationship between leaf area and sapwood area was investigated. Exposure to elevated [CO₂] doubled photosynthetic rates in current-year shoots and, despite some downregulation, 1-yr-old E shoots also had higher rates of photosynthesis than their A counterparts. Thus, the amount of assimilate fixed by E branches was substantially more than that fixed by A branches; however, this increase in the local production of assimilate did not lead to an increase in non-structural carbohydrate or stimulate growth or meristematic activity within the E branches. There was a very consistent relationship between leaf area and stem cross-sectional area that was not influenced by [CO₂]. However, unbagged branches had thicker stems than bagged branches, resulting in a slightly lower ratio of leaf area to cross-sectional area. The implications of the results for the modelling of growth and allocation and the potential utility of the branch bag technique are discussed.

KEYWORDS: ALLOCATION, ASSIMILATION, CO₂- ENRICHMENT, MORPHOLOGY, NUTRITION, PHOTOSYNTHETIC ACCLIMATION, PINE, RESISTANCE, STOMATAL CONDUCTANCE, TREES

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Barton, C.V.M., H.S.J. Lee, and P.G. Jarvis. 1993. A branch bag and CO₂ control-system for long-term CO₂ enrichment of mature sitka spruce [*Picea-sitchensis* (bong) carr]. *Plant, Cell and Environment* 16(9):1139-1148.

This paper describes the construction and performance of branch bags and a CO₂ control system used to fumigate branches of mature Sitka spruce trees with air enriched in CO₂ (700 μmol mol⁻¹). It contains some examples of results obtained using the system over the course of the first two growing seasons. The branch bags have run continuously for 2 years with very few problems. CO₂ concentrations were within 20 μmol mol⁻¹ of the target concentration for more than 90% of the time. Temperatures within the bags were slightly higher than ambient (1-2 degrees C) and this had some effect on phenology. Attenuation of quantum flux density (photosynthetically active radiation) was 10-15%. The branch bag system has enabled investigation into the effects of elevated CO₂ on mature tissue without the problems and expense of fumigating whole trees. Growth in elevated CO₂ resulted in an increase in starch and a decrease in soluble protein content of needles. Stomatal

conductance was higher in elevated CO₂ grown needles, and there was some evidence of an increase in photosynthetic capacity.

KEYWORDS: TREES

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Basile, G., M. Arienzo, and A. Zena. 1993. Soil nutrient mobility in response to irrigation with carbon-dioxide enriched water. *Communications in Soil Science and Plant Analysis* 24(11-12):1183-1195.

In our experiments, carbonated water (CW) modified the equilibria in soil. Application of CW decreased the soil pH about 1.5 units one hour after irrigation ended. Minimal, though well defined, differences in soil pH were observed between the two carbonated treatments. The same relationship between the treatments was not found in pH levels of the leachate. This seems strictly related to the temporal and spatial changes in the carbon dioxide (CO₂) acidifying effect caused by chemical and biological factors as water descended the soil column. The temporary reduction in soil pH in the CW treatment induced the highest nutrient mobility for most of the elements.

KEYWORDS: CO₂

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BassiriRad, H., K.L. Griffin, J.F. Reynolds, and B.R. Strain. 1997. Changes in root NH₄⁺ and NO₃⁻ absorption rates of loblolly and ponderosa pine in response to CO₂ enrichment. *Plant and Soil* 190(1):1-9.

Root growth and physiological uptake capacity for NH₄⁺ and NO₃⁻ were examined for seedlings of loblolly and ponderosa pine grown for 160 days under two CO₂ levels, ambient (35 Pa) and ambient plus 35 Pa (70 Pa). Fraction of biomass allocated to active fine roots as well as total N (NH₄⁺ + NO₃⁻) absorption per unit root dry mass were unaffected by CO₂. On a whole-plant basis, elevated CO₂ led to a significant increase in N acquisition in loblolly but not in ponderosa pine. However, even in loblolly pine where CO₂ significantly increased plant N acquisition, the relative increase, in biomass far exceeded the gain in N, i.e. a 60% increase in total dry weight was accompanied by only a 30% increase in N gain in response to high CO₂. We suggest that the commonly reported decline in tissue N concentration of these and other species at high CO₂ is largely caused by inability of the root systems to sufficiently compensate for increased N demand. Elevated CO₂ significantly altered root uptake capacity of the different N forms, i.e., high CO₂ significantly increased NO₃⁻ absorption rates, but decreased NH₄⁺ absorption rates in both species though the decrease in loblolly was insignificant. However, elevated CO₂ increased root respiration rate in loblolly pine while significantly decreasing it in ponderosa pine. This indicates that CO₂-induced changes in plant preference for inorganic N forms is not simply regulated by root energy status. If changes in plant preference for inorganic N forms represent typical responses to elevated CO₂, the results could have important implications for N dynamics in managed and natural plant communities.

KEYWORDS: AMMONIUM, AVAILABILITY, BARLEY, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO₂, GROWTH, L SEEDLINGS, NITRATE ABSORPTION, NITROGEN CONCENTRATION, PLANT NUTRITION

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BassiriRad, H., K.L. Griffin, B.R. Strain, and J.F. Reynolds. 1996. Effects of CO₂ enrichment on growth and root (NH₄⁺)-N-15 uptake rate of loblolly pine and ponderosa pine seedlings. *Tree Physiology* 16(11-12):957-962.

We examined changes in root growth and (NH₄⁺)-N-15 uptake capacity of loblolly pine (*Pinus taeda* L.) and ponderosa pine (*Pinus ponderosa* Douglas. Ex Laws.) seedlings that were grown in pots in a phytotron at CO₂ partial pressures of 35 or 70 Pa with NH₄⁺ as the sole N source. Kinetics of N-15-labeled NH₄⁺ uptake were determined in excised roots, whereas total NH₄⁺ uptake and uptake rates were determined in intact root systems following a 48-h labeling of intact seedlings with N-15. In both species, the elevated CO₂ treatment caused a significant downregulation of (NH₄⁺)-N-15 uptake capacity in excised roots as a result of a severe inhibition of the maximum rate of root (NH₄⁺)-N-15 uptake (V-max). Rates of (NH₄⁺)-N-15 uptake in intact roots were, however, unaffected by CO₂ treatment and were on average 4- to 10-fold less than the V-max in excised roots, suggesting that (NH₄⁺)-N-15 absorption from the soil was not limited by the kinetics of root (NH₄⁺)-N-15 uptake. Despite the lack of a CO₂ effect on intact root absorption rates, (NH₄⁺)-N-15 uptake on a per plant basis was enhanced at high CO₂ concentrations in both species, with the relative increase being markedly higher in ponderosa pine than in loblolly pine. High CO₂ concentration increased total (NH₄⁺)-N-15 uptake and the fraction of total biomass allocated to fine roots (< 2 mm in diameter) to a similar relative extent. We suggest that the increased uptake on a per plant basis in response to CO₂ enrichment is largely the result of a compensatory increase in root absorbing surfaces.

KEYWORDS: AMMONIUM, CARBON-DIOXIDE CONCENTRATION, DRY-MATTER, ELEVATED CO₂, LIMITATION, NITROGEN, NUTRITION, PHOTOSYNTHESIS, PLANTS, RESPONSES

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Bassirirad, H., J.F. Reynolds, R.A. Virginia, and M.H. Brunelle. 1997. Growth and root NO₃⁻ and PO₄³⁻ uptake capacity of three desert species in response to atmospheric CO₂ enrichment. *Australian Journal of Plant Physiology* 24(3):353-358.

In a phytotron experiment, we examined growth and rates of NO₃⁻ and PO₄³⁻ uptake in seedlings of two desert C-3 shrubs (*Larrea tridentata* and *Prosopis glandulosa*) and a desert C-4 perennial grass (*Bouteloua eriopoda*) grown under CO₂ partial pressures of 35 or 70 Pa. Plants were grown in soil but uptake studies were conducted on roots of intact seedlings placed in nutrient solutions containing both NO₃⁻ and PO₄³⁻. Elevated CO₂ increased total biomass by 69 and 55% in *Larrea* and *Prosopis* seedlings and by 25% in *Bouteloua*. NO₃⁻ and PO₄³⁻ uptake rates were more than doubled in *Bouteloua* at high compared to ambient CO₂. In contrast, CO₂ enrichment inhibited root NO₃⁻ uptake capacity in *Larrea* by about 55% without a significant effect on PO₄³⁻ absorption rate; rates of NO₃⁻ and PO₄³⁻ uptake in *Prosopis* were insensitive to CO₂ treatment. Elevated CO₂ enhanced the proportion of biomass allocated to the fine roots in *Bouteloua* but markedly reduced this fraction in *Larrea* and *Prosopis*. Foliar N concentration of both shrubs decreased in response to elevated CO₂, but was unaffected in *Bouteloua*. We suggest that compensatory changes in root size and activity are critical in determining interspecies variation in plant nutrient relations under high CO₂.

KEYWORDS: CARBON DIOXIDE, COMPETITION, DRY-MATTER, ELEVATED CO₂, MINERAL NUTRITION, NITROGEN, PHOSPHATE, PLANTS, RHIZOSPHERE, SEEDLINGS

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Bassirirad, H., R.B. Thomas, J.F. Reynolds, and B.R. Strain. 1996. Differential responses of root uptake kinetics of NH₄⁺ and NO₃⁻ to enriched atmospheric CO₂ concentration in field-grown loblolly pine. *Plant, Cell and Environment* 19(3):367-371.

The nitrogen requirement of plants is predominantly supplied by NH₄⁺ and/or NO₃⁻ from the soil solution, but the energetic cost of uptake and

assimilation is generally higher for NO₃⁻ than for NH₄⁺. We found that CO₂ enrichment of the atmosphere enhanced the root uptake capacity for NO₃⁻, but not for NH₄⁺, in field-grown loblolly pine saplings. Increased preference for NO₃⁻ at the elevated CO₂ concentration was accompanied by increased carbohydrate levels in roots. The results have important implications for the potential consequences of global climate change on plant- and ecosystem-level processes in many temperate forest ecosystems.

KEYWORDS: ABSORPTION, AMMONIUM, ASSIMILATION, BARLEY, FLUXES, FORESTS, PLANTS, RESPIRATION

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Bassirirad, H., D.T. Tissue, J.F. Reynolds, and F.S. Chapin. 1996. Response of *Eriophorum vaginatum* to CO₂ enrichment at different soil temperatures: Effects on growth, root respiration and PO₄³⁻ uptake kinetics. *New Phytologist* 133(3):423-430.

In a phytotron experiment, we examined responses of a tussock sedge, *Eriophorum vaginatum* L., to changes in atmospheric CO₂ concentration and soil temperature. We were particularly interested in phosphorus (P) acquisition and below ground plant characteristics that regulated its uptake in response to CO₂ enrichment. Plants were grown at two CO₂ partial pressures, 35 and 70 Pa, three soil temperature regimes, 5, 15 and 25 degrees C and a constant ambient air temperature of 15 degrees C. Elevated CO₂ increased total plant biomass production, but decreased tissue P concentration. Although high CO₂ enhanced root carbohydrate concentration, it inhibited root respiration with no significant effect on root PO₄³⁻ absorption capacity or root:shoot ratio. Surprisingly, there were no significant interactions between CO₂ and soil temperature. The inability of *Eriophorum* to exhibit root-level compensatory adjustments, e.g. increased root:shoot ratio or PO₄³⁻ absorption capacity, was largely responsible for the observed decline in tissue P concentration under elevated CO₂ conditions. This could ultimately limit long-term growth responses of *Eriophorum* to CO₂ enrichment in the field where P availability is limiting. We found that uptake of PO₄³⁻ in response to elevated CO₂ was independent of changes in root respiration, but changes in root respiration could have important implications for ecosystem carbon budget under elevated CO₂ levels. Our data indicated that although root respiration on a per unit biomass basis declined in response to CO₂ enrichment, this effect was counterbalanced by increased root biomass, so that high CO₂ stimulated root respiration on a whole-plant basis by 30%. This might help to explain why long-term exposure to high CO₂ increases CO₂ efflux from *Eriophorum*-dominated ecosystems.

KEYWORDS: ALASKAN TUSsock TUNDRA, CARBON DIOXIDE, ECOSYSTEMS, ELEVATED CO₂, NITROGEN, NUTRIENT ACQUISITION, NUTRITION, PHOSPHATE ABSORPTION, PHOTOSYNTHESIS, PLANTS

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Bassman, J.H., and J.C. Zwier. 1991. Gas-exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa* X *Populus deltoides* clones. *Tree Physiology* 8(2):145-159.

Responses of net photosynthesis, dark respiration, photorespiration, transpiration, and stomatal conductance to irradiance, temperature, leaf-to-air vapor density difference (VDD), and plant water stress were examined in two *Populus trichocarpa* clones (one from a moist, coastal climate in western Washington and one from a dry, continental climate in eastern Washington), one *P. deltoides* clone, and two *P. trichocarpa* x *P. deltoides* clones. Light saturation of photosynthesis in greenhouse-grown trees occurred at about 800- μ -mol m⁻² s⁻¹ for *P. deltoides*, *P. trichocarpa* x *P. deltoides*, and the eastern Washington ecotype of *P. trichocarpa*, but at about 600- μ -mol m⁻² s⁻¹ for the western

Washington ecotype of *P. trichocarpa*. Average net photosynthesis (at saturating irradiance and the optimum temperature of 25-degrees-C) was 20.7, 18.8, 18.2 and 13.4- $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *P. deltoides*, *P. trichocarpa* x *P. deltoides*, and the eastern and western Washington clones of *P. trichocarpa*, respectively. In all clones, net photosynthesis decreased about 14% as VDD increased from 3 to 18 g H₂O m⁻³. Stomatal conductance decreased sharply with decreasing xylem pressure potential (XPP) in all clones except the western Washington clone of *P. trichocarpa*. Stomata in this clone were insensitive to changes in XPP and did not control water loss. Complete stomatal closure (stomatal conductance < 0.05 cm s⁻¹) occurred at about -2.0 MPa in the eastern Washington clone of *P. trichocarpa* and around -1.25 MPa in the *P. deltoides* and *P. trichocarpa* x *P. deltoides* clones. Transpiration rates were highest in the *P. trichocarpa* x *P. deltoides* clone and lowest in the western Washington clone of *P. trichocarpa*. The *P. deltoides* clone and eastern Washington clone of *P. trichocarpa* had the highest water use efficiency (WUE) and the western Washington clone of *P. trichocarpa* had the lowest WUE. The hybrids were intermediate. It was concluded that: (1) gas exchange characteristics of eastern and western Washington clones of *P. trichocarpa* reflected adaptation to their native environment; (2) crossing the western Washington clone of *P. trichocarpa* with the more drought resistant *P. deltoides* clone produced plants better adapted to the interior Pacific Northwest climate, although the stomatal response to soil water deficits in the hybrid was conservative compared with that of the eastern Washington clone of *P. trichocarpa*; and (3) introducing eastern Washington clones of black cottonwood into breeding programs is likely to yield lines with favorable growth characteristics combined with enhanced WUE and adaptation to soil water deficits.

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Bassow, S.L., K.D.M. McConnaughay, and F.A. Bazzaz. 1994. The response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecological Applications* 4(3):593-603.

Mean global temperatures have been predicted to increase in the next century, if so the frequency of extreme temperature events may also increase. Extreme temperatures may damage plant tissue and consequently limit the survival of certain plant species in a region. Elevated concentrations of CO₂ in the atmosphere alter plant allocation, physiology, and growth, and may accentuate or ameliorate the damage from extreme temperatures. In this paper we explore the interactive effects of atmospheric CO₂ concentration, nutrient levels, and exposure to extreme temperatures on seedlings of three species of temperate deciduous trees. A 1-d exposure to extreme heat (45-degrees-C) significantly decreased conductance the following day and decreased biomass as measured at both 35 and 105 d following the extreme temperature event, regardless of atmospheric CO₂ concentration. The most shade-tolerant species, striped maple, was most severely impacted by the extreme heat event in both CO₂ environments. Furthermore, striped maple seedlings grown in elevated CO₂ concentrations had a significantly greater decrease in biomass due to the extreme heat event as compared with striped maple plants grown in ambient CO₂ concentrations at 35 d after the heat event; however, at the end of the growing season at 105 d post treatment, this difference was not significant. A one-night exposure to low temperatures (4- degrees-C) did not affect biomass for any of these species. With an increase in global mean temperatures, the frequency of extreme temperature events, particularly hot weather events, may increase and may extend to shaded understory sites. If the frequency of extremely high temperatures increases, the role that temperature extremes may play in changing competitive interactions and thus affecting community composition may increase in importance, as these temperatures appear to severely alter plant survival and growth in some species.

KEYWORDS: ATMOSPHERIC CO₂, CLIMATE, ECOSYSTEMS, ENRICHMENT, FOLIAGE TEMPERATURE, HEAT-SHOCK

PROTEINS, NIGHT TEMPERATURE, PLANTS, THERMOTOLERANCE, VARIABILITY

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Batjes, N.H. 1998. Mitigation of atmospheric CO₂ concentrations by increased carbon sequestration in the soil. *Biology and Fertility of Soils* 27(3):230-235.

The International Panel on Climate Change distinguished three main options for the mitigation of atmospheric CO₂ concentrations by the agricultural sector: (1) reduction of agriculture-related emissions, (2) creation and strengthening of C sinks in the soil, and (3) production of biofuels to replace fossil fuels. Options for sustained sequestration of C in the soil through adapted management of land resources are reviewed in the context of the ongoing discussion on the need to reduce greenhouse gas concentrations in the atmosphere. Enhanced sequestration of atmospheric CO₂ in the soil, ultimately as stable humus, may well prove a more lasting solution than (temporarily) sequestering CO₂ in the standing biomass through reforestation and afforestation. Such actions will also help to reverse processes of land degradation, thus contributing to sustained food productivity and security for the people in the regions concerned.

KEYWORDS: C STORAGE, CYCLE, DECOMPOSITION, ELEVATED CO₂, FERTILIZATION, MANAGEMENT, NITROGEN, ORGANIC-MATTER, TURNOVER, WORLD

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Battaglia, M., and P.J. Sands. 1998. Process-based forest productivity models and their application in forest management. *Forest Ecology and Management* 102(1):13-32.

Few process-based forest productivity models have become incorporated into forest management systems. The prevalent perception is that process-based models are suited only for research applications and that management questions will be solved only by using descriptive empirical models. This is despite the fact that the latter can neither deal satisfactorily with changing environmental and management conditions nor answer all questions currently asked by managers. This paper develops the proposition that the end-use specifies the design and scale of forest simulation models, and that given the range of questions now asked in forest management a range of models is required. The spatial and temporal resolution, and the input and output data required to address typical forest management questions is examined. A survey of recent literature examines in which areas, and by whom, existing forest productivity models are being applied. It is concluded that many current management questions can be adequately answered using models in which a phenomenological approach is applied to predict annual forest growth at the stand-scale. Lumped-parameter process-based models and hybrid models provide the most immediate means through which our understanding of the biological processes underlying forest growth can be included in forest management systems. However, more detailed process-based models can play an important role in validating simpler models, in the development of generalizations applicable over long time scales and for testing hypotheses about the way trees function and respond to interacting stresses. Guidelines are also given on model structures appropriate for different classes of management questions. (C) 1998 Elsevier Science B.V.

KEYWORDS: DECISION-SUPPORT SYSTEMS, DOUGLAS-FIR, DRY-MATTER ACCUMULATION, ELEVATED CO₂, GROWTH-MODELS, ORIENTED GROWTH, PINUS-RADIATA, SITE INDEX, SPRUCE, YIELD

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Batts, G.R., R.H. Ellis, J.I.L. Morison, and P. Hadley. 1998. Canopy development and tillering of field-grown crops of two contrasting cultivars of winter wheat (*Triticum aestivum*) in response to CO₂ and temperature. *Annals of Applied Biology* 133(1):101-109.

Elevated CO₂ (691 cf. 371 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$) and warmer temperatures (over the range 1.0 degrees C below to 1.6 degrees C above ambient) increased light interception by crops of two contrasting cultivars (Hereward and Soissons) of winter wheat (*Triticum aestivum* L.) during winter growth in the field. The fractional interception of light by the canopy increased more rapidly initially in Soissons than in Hereward, but Hereward showed a much greater response to CO₂ (35% increase in Hereward but only 7% in Soissons) at 500 degrees C d after sowing. By terminal spikelet formation, in contrast, fractional interception was greater in Hereward than in Soissons, while the effect of CO₂ was the same in both cultivars (9%). Thus, although differences in the relative response of canopy development to CO₂ were detected between cultivars initially, differences were negligible during later development. The greater interception of light by the canopy in elevated CO₂, at any one temperature, resulted from increased tillering. The number of tillers plant⁻¹ at terminal spikelet was a linear function of main stem dry mass at this developmental stage but with a greater response in elevated CO₂, viz 2.3 and 3.8 tillers g⁻¹ main stem dry mass at 371 and 691 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$, respectively; these relations were unaffected by cultivar.

KEYWORDS: YIELD

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Batts, G.R., R.H. Ellis, J.I.L. Morison, P.N. Nkemka, P.J. Gregory, and P. Hadley. 1998. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO₂ and temperature in field studies using temperature gradient tunnels. *Journal of Agricultural Science* 130:17-27.

Diverse cultivars of winter wheat (*Triticum aestivum* L.) were grown in the field in 1993/94 and 1994/95 at Reading UK in temperature gradient tunnels at normal atmospheric (c. 370) or elevated CO₂ concentration (c. 700 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$). In 1993/94, grain yield of cv. Avalon was insensitive to mean temperature (between 8.8 and 10.9 degrees C), while elevated CO₂ increased yield by 1.3 t ha⁻¹ (12.6%). In all other cultivars, warming reduced grain yield and CO₂ increased grain yield. In 1993/94, in cvs Galahad and Mercia the effects of CO₂ and temperature on yield were additive. However, for cv. Hereward in both years and for cv. Soissons in 1994/95, there were negative interactions between the effects of CO₂ and temperature on yield: the maximum benefit of doubling CO₂ to grain yield, 4.5 and 2.7 t ha⁻¹ (65 and 29%) respectively, occurred at cooler temperatures; there was no benefit from doubling CO₂ (i.e. 0%) once the temperature had increased above the seasonal mean by 2.2-2.6 degrees C in cv. Hereward and by 1.3 degrees C in cv. Soissons. The beneficial effect of doubling CO₂ on grain yield in cvs Galahad, Hereward, Mercia and Soissons was negated by an increase in mean seasonal temperature of only 0.7-2.0 degrees C. Warming decreased root dry mass at anthesis in 1994/95 while it increased at elevated CO₂ (49 and 186%, coolest and warmest regime, respectively). Carbon partitioned to roots declined progressively with warming, while at elevated CO₂ there was an average of 56% increase in allocation to roots. The relative impacts of both CO₂ and temperature were greater on root dry mass than on either grain yield or total above-ground biomass, while the effects on grain and biomass yield varied considerably between cultivars, suggesting that the impact of rising CO₂ and temperature are likely to be dependent on cultivar.

KEYWORDS: CARBON DIOXIDE, DURATION, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, PLANT-RESPONSES, PRODUCTIVITY, ROOT-GROWTH, SYSTEM, TRITICUM-AESTIVUM CROPS

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Batts, G.R., J.I.L. Morison, R.H. Ellis, P. Hadley, and T.R. Wheeler. 1997. Effects of CO₂ and temperature on growth and yield of crops of winter wheat over four seasons. *European Journal of Agronomy* 7(1-3):43-52.

Crops of winter wheat (*Triticum aestivum* L. cv. Hereward) were grown in the field in four consecutive seasons from 1991/1992 to 1994/1995 at Reading, UK, within polyethylene-covered tunnels along which a temperature gradient was superimposed on the ambient temperature variation at normal atmospheric (ca. 370) or an increased [CO₂] (ca. 700 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$), producing many environments from one sowing date in each season at one location. Mean seasonal temperatures varied by up to 4 degrees C along the temperature gradient. Increased [CO₂] had no effect on crop duration, or on the rate of reproductive development, which had the same temperature sensitivity across all years. A 2 degrees C warming, on the 4-year ambient mean temperature (10 degrees C), reduced crop duration by 42 days (from 254), and reduced the reproductive phase by 16 days (from 130). Crop biomass generally declined with increase in mean temperature, and was greater at increased [CO₂], with the effect of increased [CO₂] varying with temperature and between years (6-34% range in relative stimulation by increased [CO₂]). Grain yield was substantially reduced by warmer temperatures, and increased by doubling [CO₂], but the effect varied greatly between years and with temperature (7-168% range). There were both positive and negative interactions of temperature and increased [CO₂] on biomass and grain yield. In all 4 years, the increase in grain yield from doubling [CO₂] was negated by an increase in mean seasonal temperature of only 1.0-2.0 degrees C. Year-to-year variation in the responses of biomass and grain yield to [CO₂] and temperature resulted from differences in environmental conditions, influencing biomass partitioning and altering the role of different yield components. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, DURATION, ELEVATED CO₂, FIELD, MODEL, PRODUCTIVITY, RESPONSES, TRITICUM-AESTIVUM CROPS, VARIABILITY

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Batts, G.R., T.R. Wheeler, J.I.L. Morison, R.H. Ellis, and P. Hadley. 1996. Developmental and tillering responses of winter wheat (*Triticum aestivum*) crops to CO₂ and temperature. *Journal of Agricultural Science* 127:23-35.

Winter wheat (*Triticum aestivum* L., cv. Hereward) was grown in the field within four double-walled polyethylene-covered tunnels along which near-linear temperature gradients were imposed at normal atmospheric or at an elevated CO₂ concentration (c. 700 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$) in 1991/92 and in a further experiment in 1992/93. Development was more rapid the warmer the temperature. In 1991/92 an increase in mean seasonal temperature of 3.5 degrees C reduced the duration from sowing to harvest maturity (the stage when grain moisture content reduced naturally to 15-18%) by c. 38 days, and reduced the duration from the double ridge stage to harvest maturity by c. 34 days. A similar difference resulted from only 1.6 degrees C warming in 1992/93. Although the range of mean seasonal temperatures differed between years, the relation between temperature and rate of development from sowing to harvest maturity was common to both years (base temperature, -0.8 degrees C; thermal time 2410 degrees C d). Carbon dioxide concentration had no effect on this relation or on that between temperature and the rate of development from solving to the double ridge stage and from the double ridge stage to harvest maturity. Carbon dioxide enrichment increased tillering substantially in 1991/92; there were 200 more shoots m⁻² at terminal spikelet formation in crops grown at elevated compared to normal CO₂ (additional shoots were principally coleoptile tillers and those developing after tiller 2) and this

difference was reduced to 100 shoots m⁻²) approaching harvest maturity (additional shoots remaining were those developing after tiller 2). In contrast, no effect of CO₂ enrichment on tillering was detected at any stage of development in 1992/93. The number of tillers per plant at terminal spikelet formation was a linear function of main stem dry weight at this developmental stage; this relationship was not affected by year or CO₂. As CO₂ enrichment increased main stem dry weight in the first year only, when main stem dry weights at normal CO₂ were only one half of those values determined in the following year, it is concluded that any benefit of increase in CO₂ concentration to tillering in winter wheat may be greatest in those crop production environments where main stem dry weights at terminal spikelet are least and vice versa.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, ENVIRONMENT, FIELD, GROWTH, IMPACT, INITIATION, LEAF APPEARANCE, SENSITIVITY, YIELD

145

Bawa, K.S., and S. Dayanandan. 1998. Global climate change and tropical forest genetic resources. *Climatic Change* 39(2-3):473-485.

Global climate change may have a serious impact on genetic resources in tropical forest trees. Genetic diversity plays a critical role in the survival of populations in rapidly changing environments. Furthermore, most tropical plant species are known to have unique ecological niches, and therefore changes in climate may directly affect the distribution of biomes, ecosystems, and constituent species. Climate change may also indirectly affect plant genetic resources through effects on phenology, breeding systems, and plant-pollinator and plant seed disperser interactions, and may reduce genetic diversity and reproductive output. As a consequence, population densities may be reduced leading to reduction in genetic diversity through genetic drift and inbreeding. Tropical forest plants may respond to climate change through phenotypic plasticity, adaptive evolution, migration to suitable site, or extinction. However, the potential to respond is limited by a rapid pace of change and the non-availability of alternate habitats due to past and present trends of deforestation. Thus climate change may result in extinction of many populations and species. Our ability to estimate the precise response of tropical forest ecosystems to climate change is limited by lack of long-term data on parameters that might be affected by climate change. Collection of correlative data from long-term monitoring of climate as well as population and community responses at selected sites offer the most cost-effective way to understand the effects of climate change on tropical tree populations. However, mitigation strategies need to be implemented immediately. Because many effects of climate change may be similar to the effects of habitat alteration and fragmentation, protected areas and buffer zones should be enlarged, with an emphasis on connectivity among conserved landscapes. Taxa that are likely to become extinct should be identified and protected through *in situ* conservation programs.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, DRY FOREST, ELEVATED CO₂, INCOMPATIBILITY, PHENOLOGY, PLANT, RESPONSES, SYSTEMS, TREES

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Baxter, R., T.W. Ashenden, and J.F. Farrar. 1997. Effect of elevated CO₂ and nutrient status on growth, dry matter partitioning and nutrient content of *Poa alpina* var *vivipara* L. *Journal of Experimental Botany* 48(312):1477-1486.

Poa alpina var. *vivipara* L. was grown in an atmosphere containing either 340 or 680 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ within controlled environment chambers. The available nutrient regime was varied by altering the supply of nitrogen and phosphorus within a complete nutrient solution. At a high, but not low, N and P supply regime, elevated CO₂ markedly

increased growth. Differences between nutrient supply, but not atmospheric CO₂ concentration, altered the allometric relations between root and shoot. Net photosynthesis of mature leaf blades and leaf N and P concentration were reduced in plants grown at the elevated CO₂ concentration. The question was asked: is it possible to ascribe all of these effects to elevated CO₂ or are some due to nutrient deficiency caused by dilution with excess carbon? Several criteria, including the nutrient content of sink tissue, root:shoot allometry and the use of divalent cations to estimate integrated water flows are suggested in order to make this distinction. It is concluded that only at a low supply of N and P, and elevated CO₂ concentration, was low leaf N concentration due to induced nutrient deficiency. The data are consistent with a model where the capacity of sinks to use photosynthetically assimilated carbon sets both the rate of import into those sinks (and thus rate of export from source leaves) and the rate of photosynthesis of source leaves themselves.

KEYWORDS: ALLOCATION, ANTISENSE RBCS, ATMOSPHERIC CARBON-DIOXIDE, NITROGEN, PHOSPHATE STATUS, PHOSPHORUS, PHOTOSYNTHESIS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOBACCO

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Baxter, R., T.W. Ashenden, T.H. Sparks, and J.F. Farrar. 1994. Effects of elevated carbon-dioxide on 3 montane grass species .1. Growth and dry-matter partitioning. *Journal of Experimental Botany* 45(272):305-315.

Upland grasslands are a major component of natural vegetation within the UK. Such grasslands support slow growing relatively stable plant communities. The response of native montane grass species to elevated atmospheric carbon dioxide concentrations has received little attention to date. Of such studies, most have only focused on short-term (days to weeks) responses, often under favourable controlled environment conditions. In this study *Agrostis capillaris* L.(5), *Festuca vivipara* L. and *Poa alpina* L. were grown under semi-natural conditions in outdoor open-top chambers at either ambient (340 $\mu\text{mol mol}^{-1}$) or elevated (680 $\mu\text{mol mol}^{-1}$) concentrations of atmospheric carbon dioxide (CO₂) for periods from 79 to 189 d, with a nutrient availability similar to that of montane *Agrostis-Fescue* grassland in Snowdonia, N. Wales. Whole plant dry weight was increased for *A. capillaris* and *P. alpina*, but decreased for *F. vivipara*, at elevated CO₂. Major components of relative growth rate (RGR) contributing to this change at elevated CO₂ were transient changes in specific leaf area (SLA) and leaf area ratio (LAR). Despite changes in growth rate at 680 $\mu\text{mol mol}^{-1}$ CO₂, partitioning of dry weight between shoot and root in plants of *A. capillaris* and *P. alpina* was unaltered. There was a significant decrease in shoot relative to root growth at elevated CO₂ in *F. vivipara* which also showed marked discoloration of the leaves and increased senescence of the foliage.

KEYWORDS: ATMOSPHERIC CO₂, CO₂- ENRICHMENT, COMMUNITIES, EXPOSURE, PHOTOSYNTHESIS, PLANTS, RESPIRATION, SENESCENCE, STRESS, TEMPERATURE

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Baxter, R., S.A. Bell, T.H. Sparks, T.W. Ashenden, and J.F. Farrar. 1995. Effects of elevated CO₂ concentrations on 3 montane grass species .3. Source leaf metabolism and whole-plant carbon partitioning. *Journal of Experimental Botany* 46(289):917-929.

Agrostis capillaris L.(5), *Festuca vivipara* L. and *Poa alpina* L. were grown in outdoor open-top chambers at either ambient (340 \pm 3 $\mu\text{mol mol}^{-1}$) or elevated (680 \pm 4 $\mu\text{mol mol}^{-1}$) concentrations of atmospheric carbon dioxide (CO₂) for periods from 79-189 d. Photosynthetic capacity of source leaves of plants grown at both ambient and elevated CO₂ concentrations was measured at saturating light and

5% CO₂. Dark respiration of leaves was measured using a liquid phase oxygen electrode with the buffer solution in equilibrium with air (21% O₂, 0.034% CO₂). Photosynthetic capacity of *P. alpina* was reduced by growth at 680 $\mu\text{mol mol}^{-1}$ CO₂ by 105 d, and that of *F. vivipara* was reduced at 65 d and 189 d after CO₂ enrichment began, suggesting down-regulation or acclimation. Dark respiration of successive leaf blades of all three species was unaltered by growth at 680 relative to 340 $\mu\text{mol mol}^{-1}$ CO₂. In *F. vivipara*, leaf respiration rate was markedly lower at 189 d than at either 0 d or 65 d, irrespective of growth CO₂ concentration. There was a significantly lower total non-structural carbohydrate (TNC) concentration in the leaf blades and leaf sheaths of *A. capillaris* grown at 680 $\mu\text{mol mol}^{-1}$ CO₂. TNC of roots of *A. capillaris* was unaltered by CO₂ treatment. TNC concentration was increased in both leaves and sheaths of *P. alpina* and *F. vivipara* after 105 d and 65 d growth, respectively. A 4-fold increase in the water-soluble fraction (fructan) in *P. alpina* and in all carbohydrate fractions in *F. vivipara* accounted for the increased TNC content. In *F. vivipara* the relationship between leaf photosynthetic capacity and leaf carbohydrate concentration was such that there was a strong positive correlation between photosynthetic capacity and total leaf N concentration (expressed on a per unit structural dry weight basis), and total nitrogen concentration of successive mature leaves reduced with time. Multiple regression of leaf photosynthetic capacity upon leaf nitrogen and carbohydrate concentrations further confirmed that leaf photosynthetic capacity was mainly determined by leaf N concentration. In *P. alpina*, leaf photosynthetic capacity was mainly determined by leaf CHO concentration. Thus there is evidence for downregulation of photosynthetic capacity in *P. alpina* resulting from increased carbohydrate accumulation in source leaves. Leaf dark respiration and total N concentration were positively correlated in *P. alpina* and *F. vivipara*. Leaf dark respiration and soluble carbohydrate concentration of source leaves were positively correlated in *A. capillaris*. Changes in source leaf photosynthetic capacity and carbohydrate concentration of plants grown at ambient or elevated CO₂ are discussed in relation to plant growth, nutrient relations and availability of sinks for carbon.

KEYWORDS: ACCLIMATION, CALVIN CYCLE ENZYMES, CARBOHYDRATE CONTENT, COTTON PLANTS, DIOXIDE EFFLUX, GROWTH, HIGH ATMOSPHERIC CO₂, PHOTOSYNTHETIC OXYGEN EVOLUTION, RESPIRATION, SPINACH LEAVES

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Baxter, R., and J.F. Farrar. 1999. Export of carbon from leaf blades of *Poa alpina* L. at elevated CO₂ and two nutrient regimes. *Journal of Experimental Botany* 50(336):1215-1221.

The hypothesis was tested that, in plants of the alpine meadow grass (*Poa alpina* L.) exposed to elevated CO₂, net photosynthesis and export from source leaves is reduced as a result of feedback from sinks. Nutrient supply was used as one way of reducing photosynthesis and export. Single plants were grown in sand culture under specified controlled environmental conditions for a period of 50 d at two levels of nitrogen and phosphorus ('low': 0.2 mol m⁻³ N, 0.04 mol m⁻³ P; 'high': 2.5 mol m⁻³ N, 0.5 mol m⁻³ P). Compartmentation within, and export of carbon from, individual youngest fully expanded leaves of acclimated plants was determined using C-14 feeding and efflux plus mass balance calculations of carbohydrate export. Independent of treatment, the bulk of soluble carbohydrate (65-75%) was present as fructan, with most of the remainder being sucrose. Depending on nutrient supply, CO₂ could alter export from source leaves either by a reduction in the amount of sucrose present in a readily available pool for transport, or by altering the rate constant describing phloem loading.

KEYWORDS: ATMOSPHERIC CO₂, BARLEY, DIOXIDE, EXCISED LEAVES, GROWTH, METABOLISM, PATTERNS, TEMPERATURE, TUSsock TUNDRA

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Baxter, R., M. Gantley, T.W. Ashenden, and J.F. Farrar. 1994. Effects of elevated carbon-dioxide on 3 grass species from montane pasture. 2. Nutrient-uptake, allocation and efficiency of use. *Journal of Experimental Botany* 45(278):1267-1278.

Agrostis capillaris L.(4), *Festuca vivipara* L. and *Poa alpina* L. were grown in outdoor open-top chambers at either ambient (340 $\mu\text{mol mol}^{-1}$) or elevated (680 $\mu\text{mol mol}^{-1}$) CO₂ for periods from 79 to 189 d. Under these conditions there is increased growth of *A. capillaris* and *P. alpina*, but reduced growth of *F. vivipara*. Nutrient use efficiency, nutrient productivity (total plant dry weight gain per unit of nutrient) and nutrient allocation of all three grass species were measured in an attempt to understand their individual growth responses further and to determine whether altered nutrient-use efficiencies and productivities enable plants exposed to an elevated atmospheric CO₂ environment to overcome potential limitations to growth imposed by soil fertility. Total uptake of nutrients was, in general, greater in plants of *A. capillaris* and *P. alpina* (with the exception of N and K in the latter) when grown at 680 $\mu\text{mol mol}^{-1}$ CO₂. In *F. vivipara*, however, uptake was considerably reduced in plants grown at the higher CO₂ concentration. Overall, a doubling of atmospheric CO₂ concentration had little effect on the nutrient use efficiency or productivity of *A. capillaris*. Reductions in tissue nutrient content resulted from increased plant growth and not altered nutrient use efficiency. In *P. alpina*, potassium, magnesium and calcium productivities were significantly reduced and photosynthetic nitrogen and phosphorus use efficiencies were doubled at elevated CO₂ with respect to plants grown at ambient CO₂. *F. vivipara* grown for 189 d showed the most marked changes in nutrient use efficiency and nutrient productivity (on an extracted dry weight basis) when grown at elevated CO₂. *F. vivipara* grown at elevated CO₂, however, showed large increases in the ratio of nonstructural carbohydrate to nitrogen content of leaves and reproductive tissues, indicating a substantial imbalance between the production and utilization of assimilate.

KEYWORDS: ACQUISITION, ATMOSPHERIC CO₂, AVAILABILITY, CHENOPODIUM-ALBUM L, CO₂- ENRICHMENT, LEAF NITROGEN, NITROGEN CONCENTRATION, PHOTOSYNTHETIC ACCLIMATION, PLANT GROWTH, SOURCE-SINK RELATIONS

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Bazzaz, F.A. 1998. Tropical forests in a future climate: Changes in biological diversity and impact on the global carbon cycle. *Climatic Change* 39(2-3):317-336.

Tropical forest ecosystems are large stores of carbon which supply millions of people with life support requirements. Currently tropical forests are undergoing massive deforestation. Here, I address the possible impact of global change conditions, including elevated CO₂, temperature rise, and nitrogen deposition on forest structure and dynamics. Tropical forests may be particularly susceptible to climate change for the following reasons: (1) Phenological events (such as flowering and fruiting) are highly tuned to climatic conditions. Thus a small change in climate can have a major impact on the forest, its biological diversity and its role in the carbon cycle. (2) There are strong coevolutionary interactions, such as pollination seed dispersal, with a high degree of specialization, i.e., only certain animals can effect these activities for certain species. Global change can decouple these tight coevolutionary interactions. (3) Because of high species diversity per unit area, species of the tropical rain forest must have narrow niches. Thus changes in global climate can eliminate species and therefore reduce biological diversity. (4) Deforestation and other forms of disturbance may have significant feedback on hydrology both regionally and globally. The predicted decline in the rainfall in the Amazon Basin and the intensification of the Indian monsoon can have a large effect on water availability and floods which are already devastating low-lying areas. It is concluded that tropical forests may be very sensitive to

climate change. Under climatic change conditions their structure and function may greatly change, their integrity may be violated and their services to people may be greatly modified. Because they are large stores of great biological diversity, they require immediate study before it is too late. The study requires the collaboration of scientists with a wide range of backgrounds and experiences including biologists, climate modellers, atmospheric scientists, economists, human demographers and sociologists in order to carry out holistic and urgently needed work. Global climatic change brings a great challenge to science and to policy makers.

KEYWORDS: COOCCURRING BIRCH, DIOXIDE, ELEVATED ATMOSPHERIC CO₂, GROWTH-RESPONSE, INSECT HERBIVORE INTERACTIONS, MODEL SYSTEMS, PLANTS, RESOURCE USE, TEMPERATURE, TREE SEEDLINGS

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Bazzaz, F.A., D.D. Ackerly, F.I. Woodward, and L. Rochefort. 1992. Co₂ enrichment and dependence of reproduction on density in an annual plant and a simulation of its population-dynamics. *Journal of Ecology* 80(4):643-651.

1. Populations of an annual plant, *Abutilon theophrasti*, were grown at four densities (100, 500, 1500 and 4000 m⁻²) and two CO₂ concentrations (350 and 700 μmol l⁻¹) to examine the influence of CO₂ environment on density-dependent patterns of demography and reproduction. Variables measured included survivorship, proportion of plants flowering and fruiting, number of fruiting individuals, number of seeds per individual, total seed production per population, mean seed mass, and germination of seeds produced in each environment. 2. All variables, except the number of fruiting individuals, declined with increasing density, and at the highest density no individuals set seed. The number of fruiting individuals was highest at a density of 500m⁻². In the elevated CO₂ environment, survivorship was significantly reduced but the proportion of plants flowering and fruiting and the number of fruiting individuals in each population all increased. Total population seed production was higher in the elevated CO₂ environment at all densities, although the differences were not significant. Significant effects of CO₂ concentration were observed only for population-level variables, but not for mean individual fecundity or seed size. Seed germination declined with increasing maternal density, and no germination was recorded for seeds produced at 1500 m⁻². 3. Simple models of population dynamics, utilizing difference equations, were constructed to examine potential population-level consequences of these density and CO₂ effects. In the absence of a persistent seed pool, the simulated populations exhibited damped or stable oscillations under low germination values, but displayed non-cyclic ('chaotic') oscillations or went extinct for higher germination due to the complete failure of seed-set at high density. Because of its higher fecundity, the elevated-CO₂ population generally exhibited greater oscillations, and the critical germination value at which the simulated populations went extinct was much lower for the elevated-CO₂ than for the ambient-CO₂ population.

KEYWORDS: ABUTILON-THEOPHRASTI, COMPETITION, CYCLES, ELEVATED CO₂, GROWTH, NEIGHBORHOOD MODELS, SINGLE-SPECIES POPULATIONS

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Bazzaz, F.A., J.S. Coleman, and S.R. Morse. 1990. Growth-responses of 7 major cooccurring tree species of the northeastern united-states to elevated CO₂. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 20(9):1479-1484.

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Bazzaz, F.A., M. Jasienski, S.C. Thomas, and P. Wayne. 1995. Microevolutionary responses in experimental populations of plants to CO₂-enriched environments - parallel results from 2 model systems. *Proceedings of the National Academy of Sciences of the United States of America* 92(18):8161-8165.

Despite the critical role that terrestrial vegetation plays in the Earth's carbon cycle, very little is known about the potential evolutionary responses of plants to anthropogenically induced increases in concentrations of atmospheric CO₂. We present experimental evidence that rising CO₂ concentration may have a direct impact on the genetic composition and diversity of plant populations but is unlikely to result in selection favoring genotypes that exhibit increased productivity in a CO₂-enriched atmosphere. Experimental populations of an annual plant (*Abutilon theophrasti*, velvetleaf) and a temperate forest tree (*Betula alleghaniensis*, yellow birch) displayed responses to increased CO₂ that were both strongly density-dependent and genotype-specific. In competitive stands, a higher concentration of CO₂ resulted in pronounced shifts in genetic composition, even though overall CO₂-induced productivity enhancements were small. For the annual species, quantitative estimates of response to selection under competition were 3 times higher at the elevated CO₂ level. However, genotypes that displayed the highest growth responses to CO₂ when grown in the absence of competition did not have the highest fitness in competitive stands. We suggest that increased CO₂ intensified interplant competition and that selection favored genotypes with a greater ability to compete for resources other than CO₂. Thus, while increased CO₂ may enhance rates of selection in populations of competing plants, it is unlikely to result in the evolution of increased CO₂ responsiveness or to operate as an important feedback in the global carbon cycle. However, the increased intensity of selection and drift driven by rising CO₂ levels may have an impact on the genetic diversity in plant populations.

KEYWORDS: AMBIENT, CO₂- ENRICHMENT, COMPETITION, DENSITY, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, GROWTH-RESPONSE, NITROGEN, SEEDLINGS, SELECTION

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Bazzaz, F.A., and K.D.M. McConnaughay. 1992. Plant interactions in elevated CO₂ environments. *Australian Journal of Botany* 40(4-5):547-563.

Increasing atmospheric carbon dioxide concentrations present a novel resource condition for plant communities. In order to understand and predict how plant community structure and function may be altered in a high CO₂ world, we need to understand how interactions among neighbouring plants within a community will alter the growth and reproduction of component species. Because CO₂ is readily diffusible, plants have little influence on the CO₂ acquisition of their neighbours, except within particularly dense canopies. Thus, plants seldom compete directly for CO₂. Rather, CO₂ availability is likely to alter plant-plant interactions indirectly through its effects on plant growth and competition for other resources. As a consequence, competitive outcome under elevated CO₂ atmospheres within even simple systems is not easy to predict. For example, under some conditions, C₄ species in competitive assemblages have improved competitive ability relative to C₃ competitors as a result of CO₂ enrichment, contrary to expectations based on their photosynthetic pathways. It is now clear that individually grown plants can differ substantially from those within mono- or multispecific stands in response to CO₂ enrichment. At present, our understanding of how stands of interacting plants modify the availability of CO₂ and other resources is incomplete. We urgently need information about how elevated CO₂ atmospheres influence stand formation and population dynamics, specifically with regard to the identities, numbers, sizes and reproductive fitnesses of individuals within single and multiple species stands, if we are to make multi-generational predictions concerning the fate of populations and communities in an elevated CO₂

world.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, DECIDUOUS FOREST, ESTUARINE MARSH, OLD-FIELD PERENNIALS, QUERCUS-ALBA, SEEDLING GROWTH, SIZE HIERARCHIES, SOIL RESPIRATION, TUSSOCK TUNDRA

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Bazzaz, F.A., and S.L. Miao. 1993. Successional status, seed size, and responses of tree seedlings to CO₂, light, and nutrients. *Ecology* 74(1):104-112.

We studied how an enriched CO₂ atmosphere in a fully crossed design of light and nutrients, influenced 1 st-yr seedling growth in six New England deciduous forest tree species. The species, in the order of increasing shade tolerance, were gray birch (*Betula populifolia*), ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britton), and striped maple (*Acer pensylvanicum*). Elevated CO₂ environments significantly stimulated the seedling growth of all six species. Generally this was more pronounced in low light. The greatest stimulation was found under the condition of low light and high nutrients. However, individual species responded differently to elevated CO₂ levels. Among the three early-successional species, gray birch, ash, and red maple, a significant increase in seedling growth under elevated CO₂ conditions was found only with high nutrients. The three late-successional species grown under elevated CO₂ conditions (red oak, yellow birch, and striped maple) showed a greater percentage increase in seedling growth in low light than in high light. Thus, for the early-successional species, the degree of enhancement of seedling growth by elevated CO₂ levels was more sensitive to nutrient levels, while in the late-successional species the enhancement was more sensitive to the level of light. Moreover, species with large seeds (e.g., red oak) exhibited a greater response to elevated CO₂ levels under low light than species with small seeds (e.g., gray birch). The results emphasize the importance of plant species as well as other environmental resources in modifying the response of plants to elevated CO₂. Considering the light and nutrient environment observed in forest gaps of various sizes, the results of the present experiment suggest seedling regeneration in New England deciduous forests may be altered in a future high CO₂ environment.

KEYWORDS: ECOSYSTEMS, ELEVATED CO₂, ENRICHMENT, GROWTH-RESPONSES, LIQUIDAMBAR- STYRACIFLUA, NORTHEASTERN UNITED-STATES, PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, PLANTS, TEMPERATURE

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Bazzaz, F.A., S.L. Miao, and P.M. Wayne. 1993. CO₂-induced growth enhancements of cooccurring tree species decline at different rates. *Oecologia* 96(4):478-482.

To elucidate how enriched CO₂ atmospheres, soil fertility, and light availability interact to influence the long-term growth of tree seedlings, six co-occurring members of temperate forest communities including ash (*Fraxinus americana* L.), gray birch (*Betula populifolia*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), striped maple (*Acer pensylvanicum*), and red oak (*Quercus rubra* L.) were raised in a glasshouse for three years in a complete factorial design. After three years of growth, plants growing in elevated CO₂ atmospheres were generally larger than those in ambient CO₂ atmospheres, however, magnitudes of CO₂-induced growth enhancements were contingent on the availability of nitrogen and light, as well as species identity. For all species, magnitudes of CO₂-induced growth enhancements after one year of growth were greater than after three years of growth, though species' growth enhancements over the three years declined at different rates. These results suggest that CO₂-induced enhancements in forest

productivity may not be sustained for long periods of time. Additionally, species' differential growth responses to elevated CO₂ may indirectly influence forest productivity via long-term species compositional changes in forests.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, COOCCURRING BIRCH, ELEVATED CO₂, ENRICHMENT, PHOTOSYNTHETIC ACCLIMATION, RESPIRATION, RESPONSES, SEEDLINGS, SOURCE-SINK RELATIONS

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Beaudry, R.M. 1999. Effect of O₂ and CO₂ partial pressure on selected phenomena affecting fruit and vegetable quality. *Postharvest Biology and Technology* 15(3):293-303.

It is likely that from the time of the Roman Empire and perhaps before, people involved in the storage of plant material as food recognized that atmospheric modification can provide some benefit in improving storability. However, active, commercial modification of the atmosphere for the preservation of fresh fruit and vegetables dates to the early part of this century. Early successes with apple fruit has led to the attempt to apply modified atmospheres to a wide range of commodities. Responses to atmospheric modification are found to vary dramatically among plant species, organ type and developmental stage and include both unwanted and beneficial physiological responses. Desirable responses include a reduction in respiration, a reduction in oxidative tissue damage or discoloration, a reduction in the rate of chlorophyll degradation and a reduction in ethylene sensitivity with the concomitant reduction in the rate of ripening and other ethylene-mediated phenomena. Undesirable responses have included the induction of fermentation, the development of disagreeable flavors? a reduction in aroma biosynthesis, the induction of tissue injury and an alteration in the makeup of microbial fauna. The physiological bases for some of these responses to elevated CO₂ and reduced O₂ are discussed. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERE, BIOSYNTHESIS, BLUEBERRY FRUIT, BROCCOLI, ENERGY-CHARGE, ETHYLENE, MAIZE ROOT-TIPS, OXYGEN PARTIAL PRESSURES, POSTHARVEST DECAY, VOLATILE COMPOUNDS

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Becker, M., T.M. Nieminen, and F. Geremia. 1994. Short-term variations and long-term changes in oak productivity in northeastern France - the role of climate and atmospheric CO₂. *Annales Des Sciences Forestieres* 51(5):477-492.

A dendroecological study was carried out in 2 forests in northeastern France with the aim of identifying and quantifying possible long-term trends in the radial growth of sessile oak (*Quercus petraea* (Matt) Liebl) and pedunculate oak (*Q. robur* L.). A total of 150 sites were selected to represent the ecological diversity of these forests. An index Cd was used to correct annual ring width in order to compensate for the effect of different competition situations. The data were standardized with reference to the mean curve 'basal area increment vs cambial age'. The growth index curves revealed a strong increase in sessile oak growth (+64% during the period 1888 to 1987) as well as in that of pedunculate oak (+40%). The growth increase in the 'young' rings (<60 years) of sessile oak was +87%, and that of young rings of pedunculate oak was +49%. The corresponding increase in the 'old' rings (>65 years) was +48% and 15% respectively (not significant for the latter). It would thus appear that pedunculate oak has benefited to a lesser extent than sessile oak from the progressive changes in its environment. Years showing a strong growth decrease are more common for pedunculate oak than for sessile oak. These results are consistent with a recent hypothesis about a slow but general retreat of pedunculate oak, including severe episodic

declines, in favour of sessile oak in many regions of France. A model was created using a combination of meteorological data (monthly precipitation and temperature) starting in 1881, and increasing atmospheric CO₂ concentrations. The model explains 78.3% of the variance for sessile oak and 74.3% for pedunculate oak. This includes some monthly parameters of year *y* (year of ring formation), and also some parameters of the years *y*-1 to *y*-4 for sessile oak and *y*-1 to *y*-5 for pedunculate oak. The models satisfactorily reproduce the long-term trends and the interannual variation. The climatic variables alone (ie excluding the CO₂ concentration) were insufficient to explain the trends observed. The possible direct and indirect effects of increasing CO₂ concentration on the growth of both species are discussed.

KEYWORDS: *ABIES-ALBA MILL, CARBON DIOXIDE, FOREST, GROWTH, MOUNTAINS, PAST VITALITY, PINE, TREES, TRENDS, VEGETATION*

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Beckmann, K., C. Dzuibany, K. Biehler, H. Fock, R. Hell, A. Migge, and T.W. Becker. 1997. Photosynthesis and fluorescence quenching, and the mRNA levels of plastidic glutamine synthetase or of mitochondrial serine hydroxymethyltransferase (SHMT) in the leaves of the wild-type and of the SHMT-deficient *stm* mutant of *Arabidopsis thaliana* in relation to the rate of photorespiration. *Planta* 202(3):379-386.

The regulation by photorespiration of the transcript level corresponding to plastidic glutamine synthetase (GS-2) was investigated in the leaves of *Arabidopsis thaliana* (L.) Heynh. Photorespiration was suppressed by growing the plants in an atmosphere containing 300 Pa CO₂. Suppression of photorespiration was demonstrated by the ability of the conditionally lethal serine hydroxymethyltransferase (SHMT)-deficient *stm* mutant of *A. thaliana* to grow normally under these conditions. In contrast to previous studies with bean or pea that were performed at very high CO₂ partial pressure (2-4 kPa; Edwards and Coruzzi, 1989, *Plant Cell* 1: 241-248; Cock et al., 1991, *Plant Mol Biol* 17: 761-771), suppression of photorespiration during growth of *A. thaliana* in an atmosphere with 300 Pa CO₂ had no effect on the leaf GS-2 transcript level. In the short term, neither suppression of photorespiration induced by the transfer of air-grown *A. thaliana* plants into a CO₂-enriched atmosphere, nor an increase in the rate of photorespiration achieved by the transfer of high-CO₂-grown *A. thaliana* plants into air resulted in a change in the GS-2 mRNA level. The absence of photorespiratory ammonium release in leaves of the *stm* mutant had no effect on the GS-2 transcript level. Overall, our data argue against a control by photorespiration of the *A. thaliana* leaf GS-2 mRNA pool. In contrast, regulation of the leaf SHMT mRNA level may involve a negative feedback effect of at least one metabolite derived from the glycine/serine conversion during photorespiration, as indicated by the overexpression of SHMT transcripts in the leaves of the *stm* mutant.

KEYWORDS: *ACCLIMATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, ELEVATED CO₂, EXCHANGE, EXPRESSION, GENES, LIGHT, SUNFLOWER LEAVES, TOBACCO*

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Beer, S., and E. Koch. 1996. Photosynthesis of marine macroalgae and seagrasses in globally changing CO₂ environments. *Marine Ecology-Progress Series* 141(1-3):199-204.

Photosynthetic rates of many marine macroalgae are saturated by the present day inorganic carbon (Ci) composition of seawater, while those of seagrasses (or marine angiosperms) are CO₂-limited. In this study we attempted to simulate the Ci conditions of near-shore seawater during the time that seagrasses colonised the sea (in the Cretaceous), and compare the photosynthetic performance of representatives of the 2 plant

groups under those versus present day conditions. The results show that the seagrasses have an affinity for Ci at least as high as the algae under the low pH and high CO₂/HCO₃⁻ concentration ratios simulating near-shore areas of the Cretaceous seas, indicating that their photosynthetic capacity then matched that of macroalgae. However, in the high pH and high CO₂/HCO₃⁻ ratios of today, their affinity for Ci is lower than that of the macroalgae, and it is suggested that this deficiency renders them a lower ability for Ci utilisation. This situation may possibly be reversed again as global CO₂ levels of the atmosphere and, consequently, of near-shore marine habitats increase in the future.

KEYWORDS: *CELLS, ULVA SP*

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Berling, D.J. 1994. Modeling palaeophotosynthesis - late cretaceous to present. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 346(1318):421-432.

This paper presents an attempt to reconstruct potential changes in the photosynthetic rates of terrestrial C3 leaves over the past 120 Ma. The approach has been to couple palaeoatmospheric reconstructions of O₂, CO₂ and temperature from geochemical modelling, and an independent estimate of ancient CO₂ changes from fossil porphyrins, with a mechanistic biochemical model of C3 photosynthesis. The model accounts for the effect of each of these palaeoenvironmental changes, at the biochemical level, to predict leaf photosynthesis and has been parametrized for a typical gymnosperm and angiosperm. The results indicate clear potential for increased photosynthetic C3 fixation in the warm Cretaceous for both angiosperms and gymnosperms, despite the increased O₂ content of the atmosphere prevailing at the time. Photosynthetic rates are then predicted to progressively decline into the Tertiary, as a result of global cooling. The model simulations also point towards some leaf-level ecophysiological explanations for the rise in angiosperm dominance and the concomitant decline in gymnosperms from the late Cretaceous onwards, at mid-latitudes, which have not been considered previously. This work provides a basis for scaling up to the canopy level to predict the primary productivity of ancient ecosystems and their possible feedback on atmospheric composition and climate.

KEYWORDS: *ATMOSPHERIC CO₂, CARBON DIOXIDE, CLIMATE CHANGE, ELEVATED CO₂, HIGH-LATITUDES, PHANEROZOIC TIME, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, TERTIARY BOUNDARY*

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Berling, D.J. 1994. Predicting leaf gas-exchange and delta-C-13 responses to the past 30000 years of global environmental-change. *New Phytologist* 128(3):425-433.

Theoretical developments in our understanding of leaf gas exchange processes and carbon isotope composition (delta(13)C) mean that it should now be possible to model their responses to global environmental change. Such a model would be of use for process-based interpretations of historical changes in leaf delta(13)C and for understanding the global stable carbon isotope balance. This paper describes the development and validation of a model towards this aim. The resulting model is used to simulate changes in leaf photosynthesis, stomatal conductance and delta(13)C of limber pine (*Pinus flexilis*) in response to the past 30000 y of global environmental change. The predictions of needle delta(13)C are in line with reported measurements of delta(13)C from fossilized *Pinus flexilis* needles preserved in packrat middens in western USA. Leaf gas exchange predictions show that the increased water use efficiency (WUE) of these trees growing in present-day environments, relative to the past, was brought about through an increase in photosynthetic rates and a decrease in stomatal conductance. This contrasts with the explanation of the recent (past 200 y) increase in the

WUE of temperate and Mediterranean ecosystems inferred from $\delta(13)C$ measurements which are predicted by the model to have arisen largely by a decrease in stomatal conductance in response to increases in the concentration of atmospheric CO_2 since the pre-industrial era. The model as described offers the potential to contribute to our understanding of vegetation effects on the global carbon isotope balance during the glacial periods, and therefore to provide a further constraint on the carbon cycle models used to explain the low concentrations of atmospheric CO_2 at these times.

KEYWORDS: ATMOSPHERIC CO_2 CONCENTRATION, C-13/C-12 RATIO, CARBON ISOTOPE DISCRIMINATION, DIOXIDE, EMPIRICAL-MODEL, ICE-CORE RECORD, LEAVES, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

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Beerling, D.J. 1996. C-13 discrimination by fossil leaves during the late-glacial climate oscillation 12-10 ka BP: Measurements and physiological controls. *Oecologia* 108(1):29-37.

The late-glacial climatic oscillation, 12-10 ka BP, is characterised in ice core oxygen isotope profiles by a rapid and abrupt return to glacial climate. Recent work has shown that associated with this cooling was a drop in atmospheric CO_2 concentration of ca. 50 ppm. In this paper, the impact of these environmental changes on C-13 discrimination is reported, based on measurements made on a continuous sequence of fossil *Salix herbacea* leaves from a single site. The plant responses were interpreted using an integrated model of stomatal conductance, CO_2 assimilation and intercellular CO_2 concentration, influenced by external environmental factors. According to the model, temperature exerts a marked influence on C-13 discrimination by leaves and the pattern of C-13 changes recorded by the fossil leaves is consistent with other palaeotemperature curves for 12-10 ka BP, particularly the deuterium isotope record from Alaskan *Salix* woods, which generally reflects ocean temperatures. The gas exchange model correctly accounts for these changes and so permits the reconstruction of ancient rates of leaf CO_2 uptake and loss of water vapour in response to the abrupt late-glacial changes in global climate and CO_2 . The approach provides the required physiological underpinning for extracting quantitative estimates of past temperatures and for contributing an ecophysiological explanation for changes in C-13 discrimination in the fossil record.

KEYWORDS: ATMOSPHERIC CO_2 , C-13/C-12 RATIOS, C-3 PLANTS, CARBON ISOTOPE DISCRIMINATION, ELEVATED CO_2 , ENVIRONMENTAL-CHANGE, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY, WESTERN NORWAY, YOUNGER DRYAS

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Beerling, D.J. 1997. Carbon isotope discrimination and stomatal responses of mature *Pinus sylvestris* L trees exposed in situ for three years to elevated CO_2 and temperature. *Acta Oecologica-International Journal of Ecology* 18(6):697-712.

The Climate Change Experiment (CLIMEX) is a unique large scale facility in which an entire undisturbed catchment of boreal vegetation has been exposed to elevated CO_2 (560 ppm) and temperature (+3 degrees C summer, +5 degrees C winter) for the past three years with all the soil-plant-atmosphere linkages intact. Here, carbon isotope composition and stomatal density have been analysed from sequential year classes of needles of mature Scots pine trees (*Pinus sylvestris* L.) to investigate the response of time-integrated water-use efficiency (WUE) and stomatal density to CO_2 enrichment and climate change. Carbon isotope discrimination decreased and WUE increased in cohorts of needles developing under increased CO_2 and temperature, compared to needles on the same trees developing in pretreatment years. Mid-season

instantaneous gas exchange, measured on the same trees for the past four years, indicated that these responses resulted from higher needle photosynthetic rates and reduced stomatal conductance. Needles of *P. sylvestris* developing under increased CO_2 and temperature had consistently lower stomatal densities than their ambient grown counterparts on the same trees. The stomatal density of *P. sylvestris* needles was inversely correlated with $\delta(13)C$ - derived WUE, implying some effect of this morphological response on leaf gas exchange. Future atmospheric CO_2 and temperature increases are therefore likely to improve the water economy of *P. sylvestris*, at least at the scale of individual needles, by affecting stomatal density and gas exchange processes.

KEYWORDS: 4-YEAR EXPOSURE, BOREAL VEGETATION, C-3 PLANTS, DENSITY, ENRICHMENT, GAS-EXCHANGE RESPONSES, LAST 3 CENTURIES, SCOTS PINE, WATER-USE EFFICIENCY, WHOLE-CATCHMENT

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Beerling, D.J. 1997. Interpreting environmental and biological signals from the stable carbon isotope composition of fossilized organic and inorganic carbon. *Journal of the Geological Society* 154:303-309.

Stable carbon isotope studies on marine and terrestrial organic and inorganic carbon provide a means for detecting global climate change and for reconstructing past concentrations of atmospheric CO_2 . Comparison between the CO_2 estimates reconstructed from carbon isotope studies for the past 150 Ma show good agreement with the predictions of a long-term carbon-cycle model based on mass-balance studies. Further, the CO_2 estimates from these sources over the entire Phanerozoic show agreement with the fossil record of leaf stomatal density change—a feature inversely related to the concentration of atmospheric CO_2 . Isotopic studies on temporal sequences of fossilized terrestrial organic matter have contributed to palaeoecological studies on shifts in the dominance of plants with the C-4 photosynthetic pathway in ecosystems and historical changes in the metabolic processes of leaves of individual species. The long-term perspective offered by these studies provides critical information for assessing the responses of biological systems to future global environmental change.

KEYWORDS: ATMOSPHERIC CO_2 , C-4 PLANTS, CLIMATE CHANGE, DIOXIDE, ELEVATED CO_2 , ICE-CORE RECORD, LATE QUATERNARY, PERMIAN TRIASSIC BOUNDARY, STOMATAL DENSITY, WATER-USE EFFICIENCY

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Beerling, D.J. 1998. The future as the key to the past for palaeobotany? *Trends in Ecology and Evolution* 13(8):311-316.

Continued increase in the concentration of atmospheric CO_2 and its possible effects on global climate has generated intense research interest on the likely responses of terrestrial plants and vegetation. Results from this new research provide quantitative information on plant function and growth in an environment with a high CO_2 concentration, but are also relevant to understanding plant growth in the distant past and to the techniques employed by palaeobotanists for reconstructing past climates from fossil plant remains. Experimental CO_2 enrichment of plants has demonstrated direct effects on leaf physiognomy, the tolerance of plants to low temperature and the relationship between tree rings, CO_2 and climate; it therefore signals the need for caution in interpreting palaeoclimates from fossils.

KEYWORDS: ATMOSPHERIC CO_2 CONCENTRATIONS, CLIMATE, EARLY TERTIARY, ELEVATED CO_2 , ENRICHMENT, FOSSIL PLANTS, FROST HARDINESS, PHOTOSYNTHESIS, TEMPERATURE, TREE GROWTH

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Beerling, D.J. 1999. Long-term responses of boreal vegetation to global change: an experimental and modelling investigation. *Global Change Biology* 5(1):55-74.

The response of boreal ecosystems to future global change is an uncertain but potentially critical component of the feedback between the terrestrial biosphere and the atmosphere. To reduce some of the uncertainties in predicting the responses of this key ecosystem, the climate change experiment (CLIMEX) exposed an entire undisturbed catchment of boreal vegetation to CO₂ enrichment (560 ppmv) and climate change (+ 5 degrees C in winter, + 3 degrees C in summer) for three years (1994-96). This paper describes the leaf metabolic responses of the vegetation to the experimental treatment and model simulations of possible future changes in the hydrological and carbon balance of the site. Randomized intervention analysis of the leaf gas exchange measurements for the dominant species indicated *Pinus sylvestris* had significantly ($P < 0.01$) higher photosynthetic rates and *Betula pubescens* and *Vaccinium myrtillus* had significantly ($P < 0.01$) lower stomatal conductances after three years treatment compared to the controls. These responses led to sustained increases in leaf water-use efficiency of all species of trees and ground shrubs, as determined from carbon isotope analyses. Photosynthesis (A) vs. intercellular CO₂ (c(i)) response curves (A/c(i) responses), RuBisCo analysis and leaf nitrogen data together suggested none of the species investigated exhibited down-regulation in photosynthetic capacity. At the whole ecosystem level, the improved water economy of the plants did not translate into increased catchment runoff. Modelling simulations for the site indicate this was most likely brought about by a compensatory increase in evapotranspiration. In terms of the carbon budget of the site, the ecosystem model indicates that increased CO₂ and temperature would lead to boreal ecosystems of the type used in CLIMEX, and typical of much of southern Norway, acting as moderate net sinks for CO₂.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, ECOSYSTEM EXPERIMENTS, ELEVATED CO₂, FOREST ECOSYSTEMS, GAS-EXCHANGE RESPONSES, PHOTOSYNTHETIC RESPONSE, RISING ATMOSPHERIC CO₂, SCOTS PINE, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

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Beerling, D.J., and W.G. Chaloner. 1993. Evolutionary responses of stomatal density to global CO₂ change. *Biological Journal of the Linnean Society* 48(4):343-353.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, FORESTS, GAS-EXCHANGE, GROWTH, INCREASE, PLANTS, POPLAR CLONES, WATER-USE EFFICIENCY

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Beerling, D.J., and W.G. Chaloner. 1993. The impact of atmospheric CO₂ and temperature-change on stomatal density - observations from *quercus-robur* lammas leaves. *Annals of Botany* 71(3):231-235.

KEYWORDS: CARBON ISOTOPES, CENTURIES, DIOXIDE, ELEVATED CO₂, GROWTH, KRAKOW REGION, PLANTS, RECORD, RESPONSES

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Beerling, D.J., and W.G. Chaloner. 1993. Stomatal density responses of Egyptian *olea-europaea* L leaves to CO₂ change since 1327 bc. *Annals of Botany* 71(5):431-435.

KEYWORDS: ATMOSPHERIC CO₂, CENTURIES, ENRICHMENT,

RECORD, VOSTOK ICE-CORE

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Beerling, D.J., W.G. Chaloner, B. Huntley, A. Pearson, and M.J. Tooley. 1991. Tracking stomatal densities through a glacial cycle - their significance for predicting the response of plants to changing atmospheric CO₂ concentrations. *Global Ecology and Biogeography Letters* 1(5):136-142.

Continued increases in the global atmospheric CO₂ concentration have been predicted from current and projected rates of fossil fuel burning. Understanding the response of stomatal density as an important ecophysiological parameter controlling the productivity of vegetation is essential if the role of plants in the global carbon budget are to be predicted. Experimental exposure of plants to elevated CO₂ regimes in controlled environment chambers can only indicate immediate, phenotypic, short-term responses. The investigation of fossil leaves of extant species growing under the different atmospheric conditions of the last glacial and deglacial transition, when evidence from an Antarctic ice core (Barnola et al., 1987) indicates CO₂ levels markedly different from pre-industrial levels, provides one means for eliciting long-term plant responses to changing CO₂ regimes. We have prepared cuticles from Quaternary leaf fossils, from which stomatal density and index can be calculated. Our preliminary results give promise of extending the record of stomatal density response back at least 10,000 years.

KEYWORDS: ENRICHMENT, ICE, RECORD

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Beerling, D.J., W.G. Chaloner, B. Huntley, J.A. Pearson, M.J. Tooley, and F.I. Woodward. 1992. Variations in the stomatal density of *salix-herbacea* L under the changing atmospheric CO₂ concentrations of late-glacial and postglacial time. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 336(1277):215-224.

The rapidly rising CO₂ concentration of the past 200 years has been shown to be accompanied by a fall in stomatal density in the leaves of temperate trees. The present study attempts to investigate the relationship of atmospheric CO₂ change and stomatal density in the arctic-alpine shrub, *Salix herbacea*, over the longer time span of 11 500 years offered by fossil leaves from post-glacial deposits. Comparisons of fossil material from Scotland and Norway are made with leaves from living populations growing in Austria, Greenland and Scotland. The Austrian material, from an altitudinal gradient between 2000 and 2670 m above sea level, gives added comparison of contemporary differences of CO₂ partial pressure with altitude. The results of our investigation indicate, rather surprisingly, that the rising CO₂ concentration of the past 11 500 years has been accompanied by an increase in the stomatal density of *S. herbacea* in contrast to the shorter-term observations on the herbarium material of temperate trees. The most likely explanation appears to centre on the temperatures and water availability of the early post-glacial environment overriding the effect of the lower CO₂ regime. However, the scale of the time interval involved may also be significant. Natural selection over the 11 500 year period concerned may have favoured a different response to what is, in effect, an acclimatory response observed in trees within the period of rapid CO₂ rise of the past 200 years.

KEYWORDS: CARBON DIOXIDE, CLIMATE, ENRICHMENT, GRADIENT, GROWTH, LEAF ANATOMY, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, WATER-USE EFFICIENCY

174

Beerling, D.J., J. Heath, F.I. Woodward, and T.A. Mansfield. 1996.

Drought-CO₂ interactions in trees: Observations and mechanisms. *New Phytologist* 134(2):235-242.

It is sometimes assumed that because increases in atmospheric CO₂ concentration usually enhance water use efficiency per unit leaf area, there will be a tendency for plants to show greater drought tolerance as well as increased biomass in the future. A critical examination of the responses to elevated CO₂ in three temperate tree species shows that this assumption might be incorrect in the case of two of them. Both beech (*Fagus sylvatica* L.) and birch (*Betula pubescens* Ehrh.) display minimal stomatal closing responses to elevated CO₂, and in the case of *F. sylvatica* the stomatal control of transpiration per unit leaf area appears to be unable to compensate for the greater development of leaf area. By contrast, the stomata of oak (*Quercus robur* L.) close appreciably in elevated CO₂, to an extent which might be sufficient to compensate for an increase in total leaf area. A simple model for the controls on water supply and consumption for the whole tree suggests that in *F. sylvatica* the potential height attainment for a given sapwood area might decrease as the atmospheric CO₂ concentration rises. The conclusions drawn from experimental data and from modelling are supported by field observations made in the UK in 1995, when the three species responded very differently to severe drought. We suggest that the progressive increase in the concentration of atmospheric CO₂ over the past 200 yr might have accentuated differences in drought sensitivity between these species.

KEYWORDS: ATMOSPHERIC CO₂, BETULA-PENDULA ROTH, ELEVATED CARBON-DIOXIDE, FAGUS-SYLVATICA, GAS-EXCHANGE, GLOBAL ENVIRONMENTAL-CHANGE, GROWTH, PHOTOSYNTHESIS, PLANT-RESPONSES, TRANSPIRATION

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Beerling, D.J., B. Huntley, and J.P. Bailey. 1995. Climate and the distribution of *Fallopia japonica* - use of an introduced species to test the predictive capacity of response surfaces. *Journal of Vegetation Science* 6(2):269-282.

The relationship between present climate and the distribution in Europe of the aggressively invasive exotic *Fallopia japonica* is described by fitting a response surface based on three bioclimatic variables: mean temperature of the coldest month, the annual temperature sum > 5 degrees C, and the ratio of actual to potential evapotranspiration. The close fit between the observed and simulated distributions suggests that the species' European distribution is climatically determined. The response surface also provides a simulation of the extent of the area of native distribution of *F. japonica* in Southeast Asia that is generally accurate, confirming the robustness of the static correlative model upon which it is based. Simulations of the potential distribution of *F. japonica* under two alternative 2 x CO₂ climate change scenarios indicate the likelihood of considerable spread into higher latitudes and possible eventual exclusion of the species from central Europe. However, despite the robustness of the response surface with present-day climate, the reliability of these simulations as forecasts is likely to be limited because no account is taken of the direct effects of CO₂ and their interaction with the species' physiological responses to climate. Similarly, no account is taken of the potential impact of interactions with 'new' species as ecosystems change in composition in response to climate change. Nevertheless, the simulations indicate both the possible magnitude of the impacts of forecast climate changes and the regions that may be susceptible to invasion by *F. japonica*.

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Beerling, D.J., and C.K. Kelly. 1997. Stomatal density responses of temperate woodland plants over the past seven decades of CO₂ increase: A comparison of Salisbury (1927) with contemporary data. *American*

Journal of Botany 84(11):1572-1583.

We investigated the possible effect of recent (1927-1995) increases in the concentration of atmospheric CO₂ on the stomatal densities of leaves of a wide range of tree, shrub, and herb species (N = 60) by making new measurements for comparison with corresponding data reported by E. J. Salisbury in 1917-a time when ice core studies indicate CO₂ concentrations similar to 55 μ L/L lower than present. A detailed intraspecific study of the herb *Mercurialis perennis* showed plants of *M. perennis* in a Cambridgeshire woodland in 1994 had significantly lower stomatal densities, irrespective of leaf insertion point, compared with their 1927 counterparts. Comparisons made across species using evolutionary comparative methods (independent contrasts revealed a significant (P < 0.01) decrease in stomatal density over the past 70 yr. The results of both the inter- and intraspecific comparisons are consistent with the hypothesis that historical CO₂ increases have influenced leaf morphology in a manner consistent with recent experiments and the palaeoecological record. Further analyses suggested that the strength of the stomatal density response was independent of life form but dependent on "exposure" and the initial leaf stomatal density. Consequently firmer predictions for future changes in stomatal density across all species, expected as a possible result of anthropogenically related CO₂ increases, may now be possible.

KEYWORDS: ATMOSPHERIC CO₂, CENTURIES, DELTA C 13, ELEVATED CO₂, ENRICHMENT, ENVIRONMENTAL-CHANGE, GAS-EXCHANGE, GROWTH, LEAF-AREA, TAXONOMIC RELATEDNESS

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Beerling, D.J., J.C. McElwain, and C.P. Osborne. 1998. Stomatal responses of the 'living fossil' *Ginkgo biloba* L. to changes in atmospheric CO₂ concentrations. *Journal of Experimental Botany* 49(326):1603-1607.

Leaf stomatal density and index of *Ginkgo biloba* L. were both significantly (P < 0.05) reduced after 3 years growth at elevated CO₂ (560 ppm), with values comparable to those of cuticles prepared from Triassic and Jurassic fossil *Ginkgo* leaves thought to have developed in the high CO₂ 'greenhouse world' of the Mesozoic. A reciprocal transfer experiment indicated that reductions in stomatal density and index irreversibly reduced stomatal conductance, particularly at low leaf-to-air vapour pressure deficits and low internal leaf CO₂ concentrations (C_i). These effects probably contributed to the high water-use efficiency of *Ginkgo* spp. in the Mesozoic relative to those of the present, as determined from carbon isotope measurements of extant and fossil cuticles.

KEYWORDS: CYCLE, DENSITY, ENVIRONMENTAL-CHANGE, LEAVES, RECORD

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Beerling, D.J., and W.P. Quick. 1995. A new technique for estimating rates of carboxylation and electron-transport in leaves of C-3 plants for use in dynamic global vegetation models. *Global Change Biology* 1(4):289-294.

The possible responses of the terrestrial biosphere to future CO₂ increases and associated climatic change are being investigated using dynamic global vegetation models (DGVMs) which include the Farquhar et al. (1980) biochemical model of leaf assimilation as the primary means of carbon capture. This model requires representative values of the maximum rates of Rubisco activity, V_{max}, and electron transport, J_{max}, for different vegetation types when applied at the global scale. Here, we describe an approach for calculating these values based on measurements of the maximum rate of leaf photosynthesis (A_{max}) and

C-13 discrimination. The approach is tested and validated by comparison with measurements of Rubisco activity assayed directly on wild-type and transgenic *Nicotiana tabacum* (tobacco) plants with altered Rubisco activity grown under ambient and elevated CO₂ mole fractions with high and low N-supply. V-max and J(max) values are reported for 18 different vegetation types with global coverage. Both variables were linearly related reinforcing the idea of optimal allocation of resources to photosynthesis (light harvesting vs. Rubisco) at the global scale. The reported figures should be of value to the further development of vegetation and ecosystem models employing mechanistic DGVMs.

KEYWORDS: ANTISENSE GENE, CARBON ISOTOPE DISCRIMINATION, CLIMATE, CO₂ CONCENTRATIONS, GROWTH, IMPACT, OXYGENASE, PHOTOSYNTHETIC RESPONSE, RBCS

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Beerling, D.J., and F.I. Woodward. 1993. Ecophysiological responses of plants to global environmental- change since the last glacial maximum. *New Phytologist* 125(3):641-648.

Ecophysiological information on the responses of plants to past global environmental changes may be obtained from Quaternary fossil leaves by measurements of (i) stomatal density, (ii) stomatal dimensions and (iii) C-13 discrimination (DELTA C-13). The stomatal density and stomatal dimensions of leaves can be used to calculate stomatal conductance, while leaf DELTA C-13 values provide independent information on stomatal conductance and plant water use efficiency. In this paper, stomatal conductance is calculated for a sequence of radiocarbon dated fossil leaves of *Salix herbacea* L. which, together with herbarium and fresh material, represents a time-series spanning from the Last Glacial Maximum (LGM) (16 500 yr BP) to the present day. The calculated values were then tested against leaf DELTA C-13 values previously reported for the same material. Our calculations show that stomatal conductance is negatively correlated with increases in atmospheric CO₂ concentration over the last 16 500 yr. This represents the first evidence of long-term response of stomatal conductance to increases in atmospheric CO₂ concentration and confirms the response observed in experimental systems exposing plants to lower-than-present CO₂ concentrations in controlled environments. The calculated decrease in conductance was positively correlated with leaf DELTA C-13 values, supporting this interpretation. The mean leaf DELTA C-13 value for the 18th and 19th centuries was significantly ($P < 0.05$) lower than the mean for the interval LGM-Holocene (10000 yr BP) implying an increase in plant water-use-efficiency over this time. These two lines of evidence, together with the stomatal density record from a glacial cycle, and experimental studies growing C₃ plants in glacial-to-present CO₂ concentrations, strongly imply that the water use efficiency of vegetation during the LGM was lower than at present and that it has increased since that time. Further evidence in support of this conclusion comes from the pattern of world vegetation types present during the LGM previously reconstructed using palaeoecological data. This evidence demonstrates that the distribution of vegetation types during the LGM was significantly different from that of the present day and showed a contraction in the area of rain forest and a major expansion of desert areas.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATION, CARBON ISOTOPE DISCRIMINATION, CLIMATE CHANGE, FORESTS, RECORD, TEMPERATURES, TRANSPIRATION, VEGETATION, VOSTOK ICE-CORE, WATER-USE EFFICIENCY

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Beerling, D.J., and F.I. Woodward. 1994. The climate-change experiment (climex) - phenology and gas- exchange responses of boreal vegetation to global change. *Global Ecology and Biogeography Letters*

4(1):17-26.

Large-scale whole ecosystem experiments will become increasingly important for predicting and testing hypotheses of complex ecosystem responses to global change. The Climate Change Experiment (CLIMEX) uses a site with an entire undisturbed boreal-forested catchment enclosed within an existing very large scale (1200m² ground area) greenhouse. In the forthcoming year temperature will be increased stepwise to +3-degrees-C in summer, +5-degrees-C in winter and the atmospheric CO₂ concentration enriched to 560 ppm which together simulate future changes in global climate and atmospheric composition predicted by GCMs. Plants growing within this low nutrient ecosystem are strongly dependent upon mycorrhizal associations for nutrient uptake and rates of nutrient uptake. Therefore it will provide an important test of current ideas concerning how mycorrhizas might modify plant responses to global change. We describe predictions of community phenology and gas exchange at the CLIMEX site; in the latter case the effects of including and excluding rates of on nutrient supply are considered. The results are discussed with reference to the opportunities presented by CLIMEX to reveal important aspects of the physiological responses of boreal ecosystems to global change.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO₂, BUDBURST, CARBON DIOXIDE, ELEVATED CO₂, PLANT-RESPONSES, PRODUCTIVITY, TREES

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Beerling, D.J., and F.I. Woodward. 1995. Leaf stable carbon-isotope composition records increased water- use efficiency of C-3 plants in response to atmospheric co₂ enrichment. *Functional Ecology* 9(3):394-401.

1. A total of 17 temperate C-3 grass and herb species were grown for 5 weeks at three mole fraction treatments of atmospheric CO₂ (350, 525 and 700 $\mu\text{mol mol}^{-1}$). Leaf stable carbon isotope compositions ($\delta(13)\text{C}$) were determined to record long-term exchange responses together with instantaneous gas exchange measurements. The isotopic composition of the atmospheric CO₂ ($\delta(13)\text{C}(a)$) integrated over the course of the CO₂ treatments was recorded biologically using the C-4 species *Zea mays*. 2. We found that increases in the mole fraction of atmospheric CO₂ above current levels resulted in a sustained increase in instantaneous (photosynthesis, A/conductance, $g(s)$) leaf water-use efficiency (IWUE), as calculated from carbon isotope-derived $p(i)/p(a)$ ratios. Grass species showed a marked decline in the magnitude of WUE increase as the CO₂ mole fraction was increased from 525 to 700 $\mu\text{mol mol}^{-1}$, a response which was absent in herb species. 3. Isotopic derivation of the ratio of intercellular CO₂ mole fraction ($p(i)$) to that in the surrounding atmosphere ($p(a)$), considered as a set point of leaf metabolism, showed no significant ($P = 0.06$) changes in response to increases in the mole fraction of CO₂, for herb and grass species. Measurements of $p(i)/p(a)$ determined from measurements of leaf gas exchange differed significantly ($P < 0.01$) from those derived from stable isotope ratios. These differences are attributed to contrasting stomatal behaviour between herb and grass species. 4. Leaf intercellular CO₂ mole fraction and previously reported above- ground biomass responses to CO₂ increases for the same species were positively correlated ($P < 0.05$). This suggests that as atmospheric CO₂ levels continue to rise species showing sustained higher rates of leaf photosynthesis, may be translated into increased productivity depending on soil water and nutrient status.

KEYWORDS: DELTA C 13, DIOXIDE, DISCRIMINATION, LEAVES, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, STOMATAL CONDUCTANCE

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Beerling, D.J., and F.I. Woodward. 1995. Stomatal responses of variegated leaves to CO₂ enrichment. *Annals of Botany* 75(5):507-511.

The responses of stomatal density and stomatal index of five species of ornamental plants with variegated leaves grown at two mole fractions of atmospheric CO₂ (350 and 700 $\mu\text{mol mol}^{-1}$) were measured. The use of variegated leaves allowed any potential effects of mesophyll photosynthetic capacity to be uncoupled from the responses of stomatal density to changes in atmospheric CO₂ concentration. There was a decrease in stomatal density and stomatal index with CO₂ enrichment on both white (unpigmented) and green (pigmented) leaf areas. A similar response of stomatal density and index was also observed on areas of leaves with pigmentation other than green indicating that any differences in metabolic processes associated with coloured leaves are not influencing the responses of stomatal density to CO₂ concentrations. Therefore the carboxylation capacity of mesophyll tissue has no direct influence on stomatal density and index responses as suggested previously (Friend and Woodward 1990 *Advances in Ecological Research* 20: 59-124), instead the responses were related to leaf structure. The stomatal characteristics (density and index) of homobaric variegated leaves showed a greater sensitivity to CO₂ on green portions, whereas heterobaric leaves showed a greater sensitivity on white areas. These results provide evidence that leaf structure may play an important role in determining the magnitude of stomatal density and index responses to CO₂ concentrations.

KEYWORDS: CHLOROPHYLL, LEAF

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Beerling, D.J., and F.I. Woodward. 1996. In situ gas exchange responses of boreal vegetation to elevated CO₂ and temperature: First season results. *Global Ecology and Biogeography Letters* 5(3):117-127.

The climate change experiment (CLIMEX) uses a large greenhouse to investigate the responses of an entire undisturbed boreal forested catchment to elevated CO₂ (560 ppm) and temperature (+3 degrees C in summer and +5 degrees C in winter) treatments. In July and September of the first season of treatment the two dominant tree species, *Pinus sylvestris* and *Betula pubescens*, and the ground shrub *Vaccinium myrtillus* all showed an increase in leaf photosynthetic rates relative to the plants growing in the control section of the greenhouse and in an outside reference catchment. Stomatal density of needles of *P. sylvestris*, and leaves of *B. pubescens* and *V. myrtillus* decreased under CO₂ enrichment and temperature increases relative to the controls. Gas exchange and stable carbon isotope measurements will be made in future growing seasons to investigate whether acclimatory adjustments in plant metabolism occur—a critical issue affecting the carbon balance of these ecosystems.

KEYWORDS: CARBON DIOXIDE, NUTRITION, PHENOLOGY, PHOTOSYNTHESIS, STOMATAL DENSITY, WATER-USE

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Beerling, D.J., and F.I. Woodward. 1996. Palaeo-ecophysiological perspectives on plant responses to global change. *Trends in Ecology and Evolution* 11(1):20-23.

Taxonomic classifications of plant species, based on morphological characteristics, provide a stable and robust approach for inferring taxonomic and phylogenetic relationships between extant and extinct species. This implies that, although evolution is a continuous process for a species, there is no whole-scale change in those suites of morphological characteristics that define higher order (genus and greater) relationships. Recent research suggests that a higher order characteristic stomatal density - may reflect not only the atmospheric CO₂ concentration during initial evolution, but may also strongly

constrain the responses of higher order plant groups to future CO₂-enrichment.

KEYWORDS: CO₂, EVOLUTION, RECORD, VASCULAR PLANTS

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Beerling, D.J., and F.I. Woodward. 1997. Changes in land plant function over the Phanerozoic: Reconstructions based on the fossil record. *Botanical Journal of the Linnean Society* 124(2):137-153.

Major fluctuations in the concentrations of atmospheric CO₂ and O₂ are predicted by historical long-term carbon and oxygen cycle models of atmospheric evolution and will have impacted directly on past climates, plant function and evolutionary processes. Here, palaeobotanical evidence is presented from the stomatal density record of fossil leaves spanning the past 400 Myr supporting the predicted changes in atmospheric CO₂. Evidence from experiments on plants exposed to long-term high CO₂ environments and the newly assembled fossil data indicate the potential for genetic modification of stomatal characters. The influence of tile changes in fossil stomatal characteristics and atmospheric composition on the rates of leaf gas exchange over the course of land plant evolution has been investigated through modelling. Three contrasting eras of plant water economies emerge in the Devonian (high), Carboniferous (low) and from the Upper Jurassic to the present-day (high but declining). These patterns of change result from structural changes of the leaves and the impact of atmospheric CO₂ and O₂ concentrations on RuBisCO function and are consistent with the fossil evidence of sequential appearances of novel plant anatomical changes. The modelling approach is tested by comparing predicted leaf stable carbon isotope ratios with those measured on fossil plant and organic material. Viewed in a geological context, current and future increases in the concentration of atmospheric CO₂ might be considered as restoring-plant function to that more typically experienced by plants over the majority of their evolutionary history. (C) 1997 The Linnean Society of London.

KEYWORDS: C-3 PLANTS, CARBON ISOTOPE DISCRIMINATION, CO₂- ENRICHMENT, EPIDERMAL STRUCTURE, LEAF, LEAVES, NORTH-AMERICA, PHOTOSYNTHESIS, RESPONSES, STOMATAL DENSITY

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Beerling, D.J., F.I. Woodward, M. Lomas, and A.J. Jenkins. 1997. Testing the responses of a dynamic global vegetation model to environmental change: a comparison of observations and predictions. *Global Ecology and Biogeography Letters* 6(6):439-450.

Dynamic global vegetation - biogeochemistry models are required to predict the likely responses of the terrestrial biosphere to anticipated future global environmental change and for improved representation of an active vegetation surface within general circulation models of the Earth's global climate system. Testing the predictions of such models is essential to their development prior to use in a predictive capacity. The climate change experiment (CLIMEX) has exposed an entire catchment of boreal vegetation to elevated CO₂ (560 ppmv) and temperature (+3 degrees C in summer, +5 degrees C in winter) for the past three years and has a considerable archive of pre-and posttreatment measurements of both CO₂ and water vapour fluxes of the vegetation, catchment runoff and soil nutrient status. These data have been used to test the predictions of the University of Sheffield dynamic global vegetation model (SDGVM) for the same site using historical records of climate as input. Comparisons of observations and predictions at the scale of individual leaves and whole ecosystems are generally favourable, increasing our confidence in the application of the model to forecasting the responses of the terrestrial biosphere to various global change scenarios. The SDGVM has been used to predict the future responses of the ecosystem

at the site into the year 2003AD. The results indicate rather small changes in leaf area index and catchment runoff but quite large increases in net primary productivity. The model predictions are now open to testing further as the CO₂ and temperature treatments continue in the CLIMEX greenhouse.

KEYWORDS: ATMOSPHERIC CO₂, BOREAL VEGETATION, CARBON BALANCE, CLIMATE CHANGE, ELEVATED CO₂, FOREST, GAS-EXCHANGE RESPONSES, SCALE, TEMPERATURE, WHOLE-CATCHMENT

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Beeson, R.C., and M.E.D. Graham. 1991. CO₂ enrichment of greenhouse roses affects neither rubisco nor carbonic-anhydrase activities. *Journal of the American Society for Horticultural Science* 116(6):1040-1045.

The effect of prolonged CO₂ enrichment on the activities of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and carbonic anhydrase (CA) of greenhouse roses were studied. Plants of *Rosa X hybrida* 'Red Success' were grown for 2 years at ambient and 900- μ l CO₂/liter during winter and spring with 75- μ mol.m⁻².s⁻¹ photosynthetically active radiation supplemental lighting for 2 years. Measurements of initial and Mg+2-Co₂-activated activities of Rubisco and CA were made during shoot development and at different positions within the plant canopy. Generally, there were no significant differences measured in the enzyme activities between the two CO₂ concentrations. The results suggest that the photosynthetic capacity did not change and that there were no characteristic adaptations to long-term growth (up to 20 weeks) at elevated CO₂ concentrations. The maintenance of Rubisco and CA activities with prolonged exposure to CO₂-enriched atmospheres is proposed as the reason for long-term yield increases in roses when grown in enriched environments.

KEYWORDS: ACCLIMATION, DIOXIDE, GROWTH, LEAVES, LONG-TERM, PHOTOSYNTHETIC REINVIGORATION, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SEEDLINGS, SHOOT DECAPITATION

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Behboudian, M.H., and R. Lai. 1994. Carbon-dioxide enrichment in virosa tomato plant - responses to enrichment duration and to temperature. *Hortscience* 29(12):1456-1459.

Responses of the tomato (*Lycopersicon esculentum* Mill. cv. Virosa) plant to elevated CO₂ concentrations applied throughout the photoperiod or part of it were studied under two temperature regimes. Plants were exposed to CO₂ at 340 (control), 700, and 1000 μ l-liter⁻¹. The highest concentration was applied only at 22/16C (day/night) and 700 μ l-liter⁻¹ at 22/16C and 25/16C. Transpiration rates were lower and photosynthetic rates were higher under elevated CO₂ than at the ambient level. Biomass production was higher only for plants grown at 700 μ l-liter⁻¹ and 25/16C. Concentrations of macronutrients were lower in plants exposed to 1000 μ l CO₂/liter than in the control plants. Intermittent CO₂ was applied using two timing methods. In method 1, plants were exposed to 4- or 8-hour high-CO₂ concentrations during their 12-hour photoperiod. In method 2, plants were exposed for 3.5 days of each week to 700 μ l CO₂/liter. Only two of the 8-hour exposures resulted in greater growth than the controls. The lack of higher growth for CO₂-enriched plants at 22/16C was attributed to a higher dark respiration rate and to respiration rate and a lack of efficient transport of photosynthates out of leaves.

KEYWORDS: AMBIENT, ATMOSPHERIC CO₂, GROWTH, PHOTOSYNTHETIC ACCLIMATION, STARCH, TRANSPIRATION, YIELD

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Behboudian, M.H., and R. Lai. 1995. Partitioning of photoassimilates in virosa tomatoes under elevated CO₂ concentration. *Journal of Plant Physiology* 147(1):43-47.

The effect of CO₂ enrichment on the distribution of assimilates in tomato plants, *Lycopersicon esculentum* Mill. cv. 'Virosa', was studied using C-14-label. Plants were defoliated except for leaves 8, 9, and 10 (numbered acropetally). Depending on the experiment, truss 1 or trusses 1 and 2 were maintained on the plant. Within a 24-h period, the labelled leaf (leaf 10) retained high levels of C-14 in both control and CO₂-enriched plants. Truss 1 was the dominant sink for both CO₂ treatments, drawing on a considerable supply of C-14 re-exported from leaf 8 and leaf 9. The stem and root were transitory sinks and had the capacity to re-export C-14 at different rates during the light and dark periods. Pattern of photoassimilate partitioning was not affected by CO₂ treatment.

KEYWORDS: ENRICHMENT, LEAVES, PATTERNS, SOURCE-SINK RELATIONSHIPS, TRANSLOCATION

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Behboudian, M.H., and C. Tod. 1995. Postharvest attributes of virosa tomato fruit produced in an enriched carbon-dioxide environment. *Hortscience* 30(3):490-491.

The effect of preharvest CO₂ enrichment (1000 μ l . liter(-1)) on postharvest quality of tomato fruit (*Lycopersicon esculentum* Mill. 'Virosa') was studied with an emphasis on soluble sugars, ripening, and mineral composition. High-CO₂ fruit had higher concentrations of sucrose, glucose, fructose, and total soluble solids than ambient-CO₂ fruit. High-CO₂ fruit also ripened more slowly and was characterized by lower respiration and ethylene production rates than ambient-CO₂ fruit. Concentrations of N, P, and K were lower in the high-CO₂ fruit than in the ambient-CO₂ fruit, whereas those of S, Ca, and Mg were the same for both treatments. Preharvest CO₂ enrichment of 'Virosa' tomato enhances fruit desirability in terms of slower postharvest ripening and higher concentrations of soluble sugars and total soluble solids.

KEYWORDS: CO₂

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Bellisario, L.M., J.L. Bubier, T.R. Moore, and J.P. Chanton. 1999. Controls on CH₄ emissions from a northern peatland. *Global Biogeochemical Cycles* 13(1):81-91.

We examined the controls on summer CH₄ emission from five sites in a peatland complex near Thompson, Manitoba, Canada, representing a minerotrophic gradient from bog to rich fen at wet sites, where the water table positions ranged from -10 to -1 cm. Average CH₄ flux, determined by static chambers on collars, ranged from 22 to 239 mg CH₄-C m⁻² d⁻¹ and was related to peat temperature. There was an inverse relationship between water table position and CH₄ flux: higher water tables led to smaller fluxes. The determination of anaerobic CH₄ production and aerobic CH₄ consumption potentials in laboratory incubations of peat samples was unable to explain much of the variation in CH₄ flux. Average net ecosystem exchange of CO₂ ranged from 1.4 to 2.5 g CO₂-C m⁻² d⁻¹ and was strongly correlated with CH₄ flux; CH₄ emission averaged 4% of CO₂ uptake. End-of-season sedge biomass was also strongly related to CH₄ flux, indicating the important role that vascular plants play in regulating CH₄ flux. Determination of isotopic signatures in peat pore water CH₄ revealed average $\delta(13)C$ values of between -50 and -73 parts per thousand and δD of between -368 and -388 parts per thousand. Sites with large CH₄ emission rates also had high CO₂ exchange rates and enriched $\delta(13)C$ CH₄

signatures, suggesting the importance of the acetate fermentation pathway of methanogenesis. Comparison of δD and $\delta^{13}C$ signatures in pore water CH_4 revealed a slope shallow enough to suggest that oxidation is not an important overall control on CH_4 emissions at these sites, though it appeared to be important at one site. Analysis of $C-14$ in pore water CH_4 showed that most of the CH_4 was of recent origin with percent of modern carbon values of between 112 and 128%. The study has shown the importance of vascular plant activities in controlling CH_4 emissions from these wetland sites through influences on the availability of fresh plant material for methanogenesis, rhizospheric oxidation, and plant transport of CH_4 .

KEYWORDS: ATMOSPHERE, CANADA, CARBON ISOTOPIC COMPOSITION, CO_2 REDUCTION, DYNAMICS, HYDROGEN, METHANE-OXIDIZING BACTERIA, ONTARIO, WATER, WETLANDS

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BenBrahim, M., D. Loustau, J.P. Gaudillere, and E. Saur. 1996. Effects of phosphate deficiency on photosynthesis and accumulation of starch and soluble sugars in 1-year-old seedlings of maritime pine (*Pinus pinaster* Ait). *Annales Des Sciences Forestieres* 53(4):801-810.

Maritime pine seedlings were grown in 4 L pots filled with coarse sand in a greenhouse. Seedlings were supplied with a nutrient solution with three different concentrations of phosphorus (0, 0.125 and 0.5 mM). After 1 year of growth, gas exchange measurements were performed on mature needles. From these measurements, the main parameters of CO_2 assimilation (the carboxylation efficiency, the apparent quantum efficiency and the maximal rate of electron transport) were estimated using the biochemical model of photosynthesis as described by Farquhar et al (1980). Leaf nonstructural carbohydrates were also analyzed. Phosphorus deficiency decreased the phosphorus foliar concentration, but did not affect foliar nitrogen concentration. The maximal rate of photosynthesis, the carboxylation efficiency and the apparent quantum efficiency decreased in phosphorus deficient seedlings. However, the maximal rate of electron transport and stomatal conductance were not affected by phosphorus supply. Low phosphorus nutrition caused a dramatic increase in foliar starch level at the end of the photoperiod. These results indicate that inadequate phosphorus nutrition principally affected the dark reactions of photosynthesis, the apparent quantum efficiency and starch accumulation.

KEYWORDS: CARBON, ELECTRON-TRANSPORT, ELEVATED CO_2 , EUCALYPTUS-GRANDIS SEEDLINGS, GAS-EXCHANGE, GROWTH, MAIZE LEAVES, PHOSPHORUS-NUTRITION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SITKA SPRUCE

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Bender, J., U. Hertstein, and C.R. Black. 1999. Growth and yield responses of spring wheat to increasing carbon dioxide, ozone and physiological stresses: a statistical analysis 'ESPACE-wheat' results. *European Journal of Agronomy* 10(3-4):185-195.

One of the major goals of the European Stress Physiology and Climate Experiment (ESPACE-wheat) was to investigate the sensitivity of wheat growth and productivity to the combined effects of changes in CO_2 concentration, ozone and other physiological stresses. Experiments were performed at different sites throughout Europe, over three consecutive growing-seasons using open-top chambers. This paper summarizes the main experimental findings of the effects of CO_2 enrichment and other factors i.e. ozone (O-3), drought stress or nitrogen supply on the biomass and yield of spring wheat (*Triticum aestivum* cv. Minaret). Final harvest data from different sites and seasons were statistically analysed: (1) to identify main effects and interactions between experimentally controlled factors; and (2) to evaluate quantitative relationships between environmental variables and biological responses. Generally, 'Minaret'

wheat did not respond significantly to O-3, suggesting that this cultivar is relatively tolerant to the O-3 levels applied. The main effect of CO_2 was a significant enhancement of grain yield and above-ground biomass in almost all experiments. Significant interactions between CO_2 and other factors were not common, although modifications in different N- and water supplies also led to significant effects on grain yield and biomass. In addition, climatic factors (in particular: mean air temperature and global radiation) were identified as important co-variables affecting grain yield or biomass, respectively. On average, the yield increase as a result of a doubling of $[CO_2]$ was 35% compared with that observed at ambient CO_2 concentrations. However, linear regressions of grain yield or above-ground biomass for individual experiments revealed a large variability in the quantitative responses of 'Minaret' wheat to CO_2 enrichment (yield increase ranging from 11 to 121%). Hence, CO_2 responsiveness was shown to differ considerably when the same cultivar of wheat was grown at different European locations. Multiple regression analyses performed to evaluate the relative importance of the measured environmental parameters on grain yield indicated that although yield was significantly related to five independent variables (24 h mean CO_2 concentration, 12 h mean O-3 concentration, temperature, radiation, and drought stress), a large proportion of the observed variability remained unexplained. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CO_2 - ENRICHMENT, CROP RESPONSES, IMPACTS, O-3, PLANT-RESPONSES, PROTECT, RADIATION, VEGETATION

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Bender, J., U. Hertstein, A. Fangmeier, M. van Oijen, H.J. Weigel, and H.J. Jager. 1998. The impact of climate change on yield of wheat in Europe: Results of the European stress physiology and climate experiment (ESPACE-wheat). *Journal of Applied Botany-Angewandte Botanik* 72(1-2):37-42.

The European Stress Physiology and Climate Experiment (ESPACE-wheat) was funded by the EU from 1994-1997. Major goals of the project were 1) to investigate by means of experiments the sensitivity of wheat growth, development and productivity to the combined effects of changes in CO_2 concentration, climatic variables and other physiological stresses, 2) to use experimental data for extension and improvement of process-based wheat simulation models, and 3) to apply models to assess the influences on crops of climatic change, CO_2 concentration and additional stresses in Europe. Experimental studies were performed at different sites in Europe through three consecutive seasons by means of open-top chambers according to a common standard protocol, and two simulation models were used for the analysis: AFRCWHEAT2 and LINTULCC. This paper summarizes the main findings of the effects of CO_2 enrichment and other factors such as ozone, drought stress or nitrogen supply on the yield response of spring wheat (*Triticum aestivum* cv. Minaret). A comparison of the measured data with the main outputs of the LINTULCC model simulations is presented. Generally, Minaret wheat did not respond significantly to ozone. CO_2 enrichment had a positive influence on grain yield in almost all experiments, however, significant interactions between CO_2 and other factors were not common. The average measured yield increase due to CO_2 doubling was 35% compared to grain yield measured at ambient CO_2 concentrations, although there was a great variability in yield responses between sites and years. LINTULCC predicted a 42% yield increase, but a much smaller variation between individual experiments. Although the effects of CO_2 and O-2 on crop growth and yield were acceptably simulated, observed process-rates often showed variation not related to light intensity, temperature, CO_2 or O-2, ie, not related to the main driving variables of the models. This unexplained variability in the measured datasets suggested a role of factors which were not accounted for in the models.

KEYWORDS: CARBON DIOXIDE, CO_2 , FIELD, GROWTH, OZONE,

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Bernstson, G.M., K.D.M. McConnaughay, and F.A. Bazzaz. 1993. Elevated CO₂ alters deployment of roots in small growth containers. *Oecologia* 94(4):558-564.

Previously we examined how limited rooting space and nutrient supply influenced plant growth under elevated atmospheric CO₂ concentrations (McConnaughay et al. 1993). We demonstrated that plant growth enhancement under elevated CO₂ was influenced more by the concentration of nutrients added to growth containers than to either the total nutrient content per pot or amount or the dimensions of available rooting space. To gain insight into how elevated CO₂ atmospheres affect how plants utilize available belowground space when rooting space and nutrient supply are limited we measured the deployment of roots within pots through time. Contrary to aboveground responses, patterns of below-ground deployment were most strongly influenced by elevated CO₂ in pots of different volume and shape. Further, elevated CO₂ conditions interacted differently with limited belowground space for the two species we studied, *Abutilon theophrasti*, a C₃ dicot with a deep taproot, and *Setaria faberii*, a C₄ monocot with a shallow fibrous root system. For *Setaria*, elevated CO₂ increased the size of the largest region of low root density at the pot surface in larger rooting volumes independent of nutrient content, thereby decreasing their efficiency of deployment. For *Abutilon*, plants responded to elevated CO₂ concentrations by equalizing the pattern of deployment in all the pots. Nutrient concentration, and not pot size or shape, greatly influenced the density of root growth. Root densities for *Abutilon* and *Setaria* were similar to those observed in field conditions, for annual dicots and monocots respectively, suggesting that studies using pots may successfully mimic natural conditions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, FIELD, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESTRICTION, SEEDLINGS, WATER RELATIONS, YIELD

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Berntson, G.M., and F.A. Bazzaz. 1996. The allometry of root production and loss in seedlings of *Acer rubrum* (Aceraceae) and *Betula papyrifera* (Betulaceae): Implications for root dynamics in elevated CO₂. *American Journal of Botany* 83(5):608-616.

Total root production (Sigma P), total root loss (Sigma L), net root production (NP), and biomass production were determined for seedlings of *Betula papyrifera* and *Acer rubrum* in ambient and elevated CO₂ environments. Sigma P, Sigma L, and NP were calculated from sequential, independent observations of root length production through plexiglass windows. Elevated CO₂ increased Sigma P, Sigma L, and NP in seedlings of *Betula papyrifera* but not *Acer rubrum*. Root production and loss were qualitatively similar to whole-plant growth responses to elevated CO₂. *Betula* showed enhanced Sigma P, Sigma L, and biomass with elevated CO₂ but *Acer* did not. However, the observed effects of CO₂ on root production and loss did not alter the allometric relationship between root production and root loss for either *Acer* or *Betula*. Thus, in this experiment, elevated CO₂ did not affect the relationship between root production and root loss. The results of this study have important implications for the potential effects of elevated CO₂ on root dynamics. Elevated CO₂ may lead to increases in root production and in root loss (turnover) where the changes in root turnover are largely a function of the magnitude of root production increases.

KEYWORDS: ATMOSPHERIC CO₂, CARBON, COOCCURRING BIRCH, ECOSYSTEMS, FINE ROOTS, GROWTH-RESPONSE, LEAF LITTER, ORGANIC-MATTER, PLANTS, SYSTEM ARCHITECTURE

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Berntson, G.M., and F.A. Bazzaz. 1996. Belowground positive and negative feedbacks on CO₂ growth enhancement. *Plant and Soil* 187(2):119-131.

In this paper we present a conceptual model of integrated plant-soil interactions which illustrates the importance of identifying the primary belowground feedbacks, both positive and negative, which can simultaneously affect plant growth responses to elevated CO₂. The primary negative feedbacks share the common feature of reducing the amount of nutrients available to plants. These negative feedbacks include increased litter C/N ratios, and therefore reduced mineralization rates, increased immobilization of available nutrients by a larger soil microbial pool, and increased storage of nutrients in plant biomass and detritus due to increases in net primary productivity (NPP). Most of the primary positive feedbacks share the common feature of being plant mediated feedbacks, the only exception being Zak et al.'s hypothesis that increased microbial biomass will be accompanied by increased mineralization rates. Plant nutrient uptake may be increased through alterations in root architecture, physiology, or mycorrhizal symbioses. Further, the increased C/N ratios of plant tissue mean that a given level of NPP can be achieved with a smaller supply of nitrogen. Identification of the net plant-soil feedbacks to enhanced productivity with elevated CO₂ are a critical first step for any ecosystem. It is necessary, however, that we first identify how universally applicable the results are from one study or one ecosystem before ecosystem models incorporate this information. The effect of elevated CO₂ on plant growth (including NPP, tissue quality, root architecture, mycorrhizal symbioses) can vary greatly for different species and environmental conditions. Therefore it is reasonable to expect that different ecosystems will show different patterns of interacting positive and negative feedbacks within the plant-soil system. This inter-ecosystem variability in the potential for long-term growth responses to rising CO₂ levels implies that we need to parameterize mechanistic models of the impact of elevated CO₂ on ecosystem productivity using a detailed understanding of each ecosystem of interest.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION, ELEVATED CO₂, ENRICHMENT, FINE ROOTS, LONG-TERM RESPONSE, NITROGEN SATURATION, PLANT, SOIL SYSTEM, TEMPERATE FOREST ECOSYSTEMS

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Berntson, G.M., and F.A. Bazzaz. 1997. Elevated CO₂ and the magnitude and seasonal dynamics of root production and loss in *Betula papyrifera*. *Plant and Soil* 190(2):211-216.

The impact of elevated atmospheric CO₂ on belowground plant growth is poorly understood relative to its effects on aboveground growth. We carried out a study of the seasonal dynamics of gross root production and death to determine how elevated CO₂ affected the dynamics of net and gross root production through a full growing season. We quantified gross root production and root loss from sequential, in situ images of fine roots of *Betula papyrifera* in ambient (375 ppm) and elevated (700 ppm) CO₂ atmospheres from 2 weeks following germination through leaf senescence. We found that elevated CO₂ led to increases in the magnitude of cumulative gross production (Sigma P) and cumulative gross loss (Sigma L) of roots. However, the effect of elevated CO₂ on these processes was seasonally dependent. Elevated CO₂ led to greater levels of enhancement in Sigma P early in the growing season, prior to maximum standing root length (NP). In contrast, elevated CO₂ led to greater levels of enhancement in Sigma L in the last half of the growing season, after maximum NP had been reached. This difference in the timing of when elevated CO₂ affects Sigma P and Sigma L led to a transitory, early enhancement in NP. By the end of the growing season, there was no significant effect of elevated CO₂ on NP, and Sigma P was 87% greater than NP for ambient CO₂ and 117% greater in elevated

CO₂. We conclude that static assessments of belowground productivity may greatly underestimate gross fine root productivity and turnover and this bias can be exaggerated with elevated CO₂.

KEYWORDS: *ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, FINE ROOTS, LENGTH, NITROGEN, NORTHERN HARDWOOD FOREST, RESPONSES, TURNOVER*

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Berntson, G.M., and F.A. Bazzaz. 1997. Nitrogen cycling in microcosms of yellow birch exposed to elevated CO₂: Simultaneous positive and negative below-ground feedbacks. *Global Change Biology* 3(3):247-258.

This study investigated simultaneous plant and soil feedbacks on growth enhancement with elevated [CO₂] within microcosms of yellow birch (*Betula alleghaniensis* Britt.) in the second year of growth. Understanding the integrated responses of model ecosystems may provide key insight into the potential net nutrient feedbacks on [CO₂] growth enhancements in temperate forests. We measured the net biomass production, C:N ratios, root architecture, and mycorrhizal responses of yellow birch, in situ rates gross nitrogen mineralization and the partitioning of available NH₄⁺ between yellow birch and soil microbes. Elevated atmospheric [CO₂] resulted in significant alterations in the cycling of N within the microcosms. Plant C/N ratios were significantly increased, gross mineralization and NH₄⁺ consumption rates were decreased, and relative microbial uptake of NH₄⁺ was increased, representing a suite of N cycling negative feedbacks on N availability. However, increased C/N ratios may also be a mechanism which allows plants to maintain higher growth with a constant or reduced N supply. Total plant N content was increased with elevated [CO₂], suggesting that yellow birch had successfully increased their ability to acquire nutrients during the first year of growth. However, plant uptake rates of NH₄⁺ had decreased in the second year. This discrepancy implies that, in this study, nitrogen uptake skewed a trend through ontogeny of decreasing enhancement under elevated [CO₂]. The reduced N mineralization and relatively increased N immobilization are a potential feedback which may drive this ontogenetic trend. This study has demonstrated the importance of using an integrated approach to exploring potential nutrient-cycling feedbacks in elevated [CO₂].

KEYWORDS: *ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION DYNAMICS, DIRECT EXTRACTION, FINE ROOTS, GROWTH ENHANCEMENT, HARDWOOD LEAF LITTER, LIGNIN CONTENT, MICROBIAL BIOMASS NITROGEN, POOL DILUTION, SOIL ORGANIC MATTER*

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Berntson, G.M., and F.A. Bazzaz. 1998. Regenerating temperate forest mesocosms in elevated CO₂: belowground growth and nitrogen cycling. *Oecologia* 113(1):115-125.

The response of temperate forest ecosystems to elevated atmospheric CO₂ concentrations is important because these ecosystems represent a significant component of the global carbon cycle. Two important but not well understood processes which elevated CO₂ may substantially alter in these systems are regeneration and nitrogen cycling. If elevated CO₂ leads to changes in species composition in regenerating forest communities then the structure and function of these ecosystems may be affected. In most temperate forests, nitrogen appears to be a limiting nutrient. If elevated CO₂ leads to reductions in nitrogen cycling through increased sequestration of nitrogen in plant biomass or reductions in mineralization rates, long-term forest productivity may be constrained. To study these processes, we established mesocosms of regenerating forest communities in controlled environments maintained at either ambient (375 ppm) or elevated (700 ppm) CO₂ concentrations.

Mesocosms were constructed from intact monoliths of organic forest soil. We maintained these mesocosms for 2 years without any external inputs of nitrogen and allowed the plants naturally present as seeds and rhizomes to regenerate. We used N-15 pool dilution techniques to quantify nitrogen fluxes within the mesocosms at the end of the 2 years. Elevated atmospheric CO₂ concentration significantly affected a number of plant and soil processes in the experimental regenerating forest mesocosms. These changes included increases in total plant biomass production, plant C/N ratios, ectomycorrhizal colonization of tree fine roots, changes in tree fine root architecture, and decreases in plant NH₄⁺ uptake rates, gross NH₄⁺ mineralization rates, and gross NH₄⁺ consumption rates. In addition, there was a shift in the relative biomass contribution of the two dominant regenerating tree species; the proportion of total biomass contributed by white birch (*Betula papyrifera*) decreased and the proportion of total biomass contributed by yellow birch (*B. alleghaniensis*) increased. However, elevated CO₂ had no significant effect on the total amount of nitrogen in plant and soil microbial biomass. In this study we observed a suite of effects due to elevated CO₂, some of which could lead to increases in potential long term growth responses to elevated CO₂, other to decreases. The reduced plant NH₄⁺ uptake rates we observed are consistent with reduced NH₄⁺ availability due to reduced gross mineralization rates. Reduced NH₄⁺ mineralization rates are consistent with the increases in C/N ratios we observed for leaf and fine root material. Together, these data suggest the positive increases in plant root architectural parameters and mycorrhizal colonization may not be as important as the potential negative effects of reduced nitrogen availability through decreased decomposition rates in a future atmosphere with elevated CO₂.

KEYWORDS: *ATMOSPHERIC CARBON-DIOXIDE, DIRECT EXTRACTION, LEAF LITTER, MICROBIAL BIOMASS NITROGEN, PLANT, POOL DILUTION, RESPONSES, SEEDLINGS, SOIL, TERRESTRIAL ECOSYSTEMS*

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Berntson, G.M., N. Rajakaruna, and F.A. Bazzaz. 1998. Growth and nitrogen uptake in an experimental community of annuals exposed to elevated atmospheric CO₂. *Global Change Biology* 4(6):607-626.

Rising levels of atmospheric CO₂ may alter patterns of plant biomass production. These changes will be dependent on the ability of plants to acquire sufficient nutrients to maintain enhanced growth. Species-specific differences in responsiveness to CO₂ may lead to changes in plant community composition and biodiversity. Differences in species-level growth responses to CO₂ may be, in a large part, driven by differences in the ability to acquire nutrients. To understand the mechanisms of how elevated CO₂ leads to changes in community-level productivity, we need to study the growth responses and patterns of nutrient acquisition for each of the species that comprise the community. In this paper, we present a study of how elevated CO₂ affects community-level and species-level patterns of nitrogen uptake and biomass production. As an experimental system we use experimental communities of 11 co-occurring annuals common to disturbed seasonal grasslands in south-western U.S.A. We established experimental communities with approximately even numbers of each species in three different atmospheric CO₂ concentrations (375, 550, and 700 ppm). We maintained these communities for 1, 1.5, and 2 months at which times we applied a N-15 tracer ((NH₄NO₃)-N-15-N-15) to quantify the nitrogen uptake and then measured plant biomass, nitrogen content, and nitrogen uptake rates for the entire communities as well as for each species. Overall, community-level responses to elevated CO₂ were consistent with the majority of other studies of individual- and multispecies assemblages, where elevated CO₂ leads to enhanced biomass production early on, but this enhancement declines through time. In contrast, the responses of the individual species within the communities was highly variable, showing the full range of responses from positive to negative. Due to the large variation in size between the

different species, community-level responses were generally determined by the responses of only one or a few species. Thus, while several of the smaller species showed trends of increased biomass and nitrogen uptake in elevated CO₂ at the end of the experiment, community-level patterns showed a decrease in these parameters due to the significant reduction in biomass and nitrogen content in the single largest species. The relationship between enhancement of nitrogen uptake and biomass production in elevated CO₂ was highly significant for both 550 ppm and 700 ppm CO₂. This relationship strongly suggests that the ability of plants to increase nitrogen uptake (through changes in physiology, morphology, architecture, or mycorrhizal symbionts) may be an important determinant of which species in a community will be able to respond to increased CO₂ levels with increased biomass production. The fact that the most dominant species within the community showed reduced enhancement and the smaller species showed increased enhancement suggest that through time, elevated CO₂ may lead to significant changes in community composition. At the community level, nitrogen uptake rates relative to plant nitrogen content were invariable between the three different CO₂ levels at each harvest. This was in contrast to significant reductions in total plant nitrogen uptake and nitrogen uptake relative to total plant biomass. These patterns support the hypothesis that plant nitrogen uptake is largely regulated by physiological activity, assuming that physiological activity is controlled by nitrogen content and thus protein and enzyme content.

KEYWORDS: ARCHITECTURE, BIODIVERSITY, CARBON DIOXIDE, ECOSYSTEMS, ENRICHMENT, GAILLARDIA-PULCHELLA, LOBLOLLY-PINE, PHLOX, PLANTS, RESPONSES

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Berntson, G.M., P.M. Wayne, and F.A. Bazzaz. 1997. Below-ground architectural and mycorrhizal responses to elevated CO₂ in *Betula alleghaniensis* populations. *Functional Ecology* 11(6):684-695.

1. Replicate populations of crowded, regenerating stands of *Betula alleghaniensis* were grown in ambient and elevated (700 p.p.m.) atmospheric CO₂ concentrations in monoliths of forest soil. Early in the second year the seedlings were harvested and detailed measurements of individual plant root architectural parameters and ectomycorrhizal colonization were made. 2. Comparing the average responses of individual plants within the populations, elevated CO₂ had no significant effects on architectural parameters that improve a plant's ability to forage for and acquire soil resources. In contrast, the intensity and magnitude of mycorrhizal colonization, and whole plant C/N ratios were significantly enhanced with elevated CO₂. 3. The allometric scaling relationship between total plant biomass and root biomass was not affected by CO₂, suggesting that relative allocation between roots and shoots was not affected. However, the allometric scaling relationships between root architectural parameters and plant biomass, and between fine root biomass and woody root biomass were significantly altered by elevated CO₂. For all of these relationships, elevated CO₂ reduced the 'size bias' of architectural components in relation to plant size within the populations; in elevated CO₂ root architectural size (e.g. root length) per unit biomass was more similar between the smallest and largest individuals within the population than was the case for ambient CO₂. 4. Overall, the results of this study suggest that the average individual seedling biomass and architectural growth responses within populations of plants exposed to elevated atmospheric CO₂ levels may be unresponsive, but that mycorrhizal responses and interactions among plants within populations may be altered significantly. These findings have important implications for how we make predictions about plant growth responses to elevated CO₂ in natural ecosystems. Significant increases in mycorrhizal infection rates and architecture-biomass allometries suggest that below-ground competitive interactions within plant populations may be reduced in elevated CO₂. Alterations in competitive interactions may lead to shifts in productivity and plant population structure.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COMPETITION, ENRICHMENT, FOREST ECOSYSTEMS, GROWTH, PLANT-ROOT SYSTEMS, QUERCUS-ALBA, SEEDLINGS, SIZE HIERARCHIES, SOIL

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Berntson, G.M., and F.I. Woodward. 1992. The root-system architecture and development of senecio- *vulgaris* in elevated CO₂ and drought. *Functional Ecology* 6(3):324-333.

1. The impact of elevated CO₂ and drought on the architecture and development of root systems of *Senecio vulgaris* was examined and implications for water and nutrient uptake discussed. Plants were grown in miniature rhizotrons to non-destructively monitor the development of roots in situ at both an elevated (700- μ -mol mol⁻¹) and ambient (350- μ -mol mol⁻¹) atmospheric CO₂ concentration and a high or a low supply of water. 2. CO₂ and water had a significant impact on the way that *S. vulgaris* root systems filled the soil matrix. Elevated CO₂ resulted in more branched, longer root systems that foraged through larger volumes of soil. Under elevated CO₂ and a low water supply, root systems had branching and foraging patterns and root length similar to those grown under ambient CO₂ with a high water supply. 3. Overall, water had a more pronounced impact on the growth rate of *S. vulgaris* roots than did CO₂. The density of rooting remained unchanged across all treatments. Thus, under elevated CO₂ the intensity of foraging *S. vulgaris* root systems might be unchanged while the extent of foraging by these root systems, as indicated by the horizontal spread of roots, may be increased.

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Berry, S.C., G.T. Varney, and L.B. Flanagan. 1997. Leaf $\delta^{13}C$ in *Pinus resinosa* trees and understory plants: Variation associated with light and CO₂ gradients. *Oecologia* 109(4):499-506.

Our objective was to evaluate the relative importance of gradients in light intensity and the isotopic composition of atmospheric CO₂ for variation in leaf carbon isotope ratios within a *Pinus resinosa* forest. In addition, we measured photosynthetic gas exchange and leaf carbon isotope ratios on four understory species (*Dryopteris carthusiana*, *Epipactis helleborine*, *Hieracium floribundum*, *Rhamnus frangula*), in order to estimate the consequence of the variation in the understory light microclimate for carbon gain in these plants. During midday, CO₂ concentration was relatively constant at vertical positions ranging from 15 m to 3 m above ground. Only at positions below 3 m was CO₂ concentration significantly elevated above that measured at 15 m. Based on the strong linear relationship between change in CO₂ concentration and $\delta^{13}C$ values for air samples collected during a diurnal cycle, we calculated the expected vertical profile for the carbon isotope ratio of atmospheric CO₂ within the forest. These calculations indicated that leaves at 3 m height and above were exposed to CO₂ of approximately the same isotopic composition during daylight periods. There was no significant difference between the daily mean $\delta^{13}C$ values at 15 m (-7.77 parts per thousand) and 3 m (-7.89 parts per thousand), but atmospheric CO₂ was significantly depleted in C-13 closer to the ground surface, with daily average $\delta^{13}C$ values of -8.85 parts per thousand at 5 cm above ground. The light intensity gradient in the forest was substantial, with average photosynthetically active radiation (PAR) on the forest floor approximately 6% of that received at the top of the canopy. In contrast, there were only minor changes in air temperature, and so it is likely that the leaf-air vapour pressure difference was relatively constant from the top of the canopy to the forest floor. For red pine and elm tree samples, there was a significant correlation between leaf $\delta^{13}C$ value and the height at which the leaf sample was collected. Leaf tissue sampled near the forest floor, on average, had lower $\delta^{13}C$ values than samples collected near the top of the canopy. We suggest that the average light intensity gradient through the

canopy was the major factor influencing vertical changes in tree leaf $\delta(13)C$ values. In addition, there was a wide range of variation (greater than 4 parts per thousand) among the four understory plant species for average leaf $\delta(13)C$ values. Measurements of leaf gas exchange, under natural light conditions and with supplemental light, were used to estimate the influence of the light microclimate on the observed variation in leaf carbon isotope ratios in the understory plants. Our data suggest that one species, *Epipactis helleborine*, gained a substantial fraction of carbon during sunflecks.

KEYWORDS: AMAZONIAN RAIN FORESTS, ATMOSPHERIC CO₂, C 13/C 12, CANOPIES, CARBON ISOTOPE DISCRIMINATION, LEAVES, PHOTOSYNTHESIS, STRATIFICATION, SUNFLECKS, VALUES

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Berryman, C.A., D. Eamus, and G.A. Duff. 1993. The influence of CO₂ enrichment on growth, nutrient content and biomass allocation of *maranthes-corymbosa*. *Australian Journal of Botany* 41(2):195-209.

Seedlings of *Maranthes corymbosa* Blume, an evergreen tree of tropical Australia and Indonesia were grown for 32 weeks under conditions of ambient and elevated (700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) CO₂ in tropical northern Australia. Seedlings were exposed to ambient temperature, vapour pressure deficit and photon flux density fluctuations. Rates of germination and percentage germination were not affected by elevated CO₂. Total plant biomass, height growth, total plant leaf area, numbers of leaves and branches and specific leaf weight were significantly increased by elevated CO₂. Root:shoot ratio and foliar P, K, Mg, Mn and Ca levels were unaffected but foliar nitrogen levels were decreased by elevated CO₂. Nutrient-use-efficiency was unaffected for phosphorus, magnesium, manganese, calcium and potassium but nitrogen-use-efficiency increased in response to elevated CO₂.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE ENRICHMENT, CARBOXYLASE, ECOLOGY, ELEVATED CO₂, FOREST, LIRIODENDRON-TULIPIFERA L, NITROGEN, PHOTOSYNTHESIS, SEEDLING GROWTH

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Berryman, C.A., D. Eamus, and G.A. Duff. 1994. Stomatal responses to a range of variables in 2 tropical tree species grown with CO₂ enrichment. *Journal of Experimental Botany* 45(274):539-546.

Seedlings of *Maranthes corymbosa* (Blume) and *Eucalyptus tetrodonta* (F. Muell) were grown with or without CO₂ enrichment (700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$). The response of stomatal conductance (g(s)) to leaf drying, exogenous abscisic acid and calcium ions was investigated in *M. corymbosa*. Reciprocal transfer experiments were also conducted whereby plants were grown in one treatment and then transferred to the other before g(s) was measured. Stomatal conductance in *M. corymbosa* was more sensitive (a greater percentage decline in g(s) per unit percentage decline in leaf fresh weight) to leaf water status under conditions of CO₂ enrichment compared to ambient conditions. However, the rate of reduction of g(s) in response to exogenous abscisic acid was not influenced by CO₂ treatment. In contrast, the rate of reduction of g(s) in response to exogenous CaCl₂ was decreased under conditions of CO₂ enrichment. Reciprocal transfer experiments showed that exposure to CO₂ enrichment results in a short-term, reversible decline in g(s) as a result of decreased stomatal aperture and a long-term, irreversible decline in g(s) as a result of a decreased stomatal density. Seedlings of *E. tetrodonta* were used to investigate the response of g(s) to light flux density, leaf-to-air vapour pressure difference (LAVPD), leaf internal CO₂ concentration (C-i) and temperature. Reciprocal transfer experiments were also conducted. CO₂ enrichment did not influence the pattern or sensitivity of response of g(s) to LAVPD and C-i

in *E. tetrodonta*. In contrast, the slope of the response of g(s) to temperature decreased for trees grown under elevated [CO₂](a) conditions and the equilibrium g(s) attained at saturating light was also decreased for plants grown under elevated [CO₂](a) conditions.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CO₂, BEHAVIOR, CALCIUM, HUMIDITY, LEAVES, PRESSURE, SOLANUM-MELONGENA, WATER-STRESS

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Bertani, A., I. Brambilla, S. Mapelli, and R. Reggiani. 1997. Elongation growth in the absence of oxygen: The rice coleoptile. *Russian Journal of Plant Physiology* 44(4):543-547.

Rice, one of the few plant species adapted to growth in wetland conditions, is able to germinate in waterlogged soils promoting only the growth of a white coleoptile in order to reach the surface of the water, contact the atmosphere, and transfer oxygen to the seed, allowing subsequent growth of the radicle and leaf. In the anoxic cells of rice coleoptiles, an efficient alcoholic fermentation allows an elevated energy charge to be maintained. Significant RNA and protein syntheses including phosphorylation and glycosylation occur too. The cytoplasmic pH is maintained at a level far from acidosis. The anoxic growth of rice coleoptiles, essentially an elongation growth, is sustained by a high turgor pressure, with free amino acids and potassium as main components. Among the metabolic processes involved in the regulation of the elongation of rice coleoptiles, a crucial role is played by amino acid metabolism and the accumulation of putrescine, which is able to stimulate plasmalemma ATPase activity. Anaerobic elongation is also stimulated in the presence of 20% CO₂ in the growth medium, inhibited by light and abscisic acid, unaffected by ethylene, and slightly promoted by auxin. The role of both metabolites and hormones along with environmental factors in maintaining cellular homeostasis and coleoptile elongation are reconsidered and discussed in Light of new data.

KEYWORDS: ACCUMULATION, ANAEROBIOSIS, ANOXIA, GERMINATION, METABOLIC-RATE, ORYZA SATIVA L, PH, POLYAMINES, PROTEIN-SYNTHESIS, SEEDLINGS

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Bertin, N., and C. Gary. 1993. Evaluation of tomgro, a dynamic-model of growth and development of tomato (*lycopersicon-esculentum* mill) at various levels of assimilate supply-and-demand. *Agronomie* 13(5):395-405.

TOMGRO, a tomato growth and development model, has been examined under different levels of assimilate source and sink activities, induced by CO₂ enrichment and truss thinning. The main purpose was the evaluation of the assumptions on dry matter partitioning and fruit setting. The photosynthesis submodel has been calibrated to fit the daily dry matter production. The main input parameters to the development and growth submodels have been experimentally measured. The calibrated model provides good simulations of the leaf area expansion, but it takes no account of the variations in the assimilates stored in leaf blades. Total fruit growth is well simulated in spite of a small underestimation for of development and simulations of source/sink balance leads to good simulations of the number of set fruits. This result confirms the hypothesis that fruit set depends on the ratio between assimilate source and sink activities. This calibration with a beef tomato cultivar proves the robustness of the model and permits some improvements to be suggested. The surplus assimilates should be stored in a pool, which could exert a buffer effect during low supply periods. Sink strength of reproductive and vegetative parts should be measured for different cultivars, and under various climatic conditions. Finally, whether the functions of assimilate distribution and fruit set are still valid under very low supply conditions or whether some organs have

priority over the others remains to be determined.

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Bertin, N., and C. Gary. 1998. Short and long term fluctuations of the leaf mass per area of tomato plants - Implications for growth models. *Annals of Botany* 82(1):71-81.

The leaf mass per unit leaf area (LMA) is a key variable in many growth models, since it is often used to predict leaf area expansion from leaf dry weight increase, or vice versa. Influences of source-sink balance on leaf area, leaf dry weight, LMA, and leaf content in non-structural carbohydrates were investigated in glasshouse tomato crops. The source-sink balance was manipulated by artificial shading, CO₂ enrichment or fruit removal using different tomato cultivars. Leaf area was hardly affected by competition for assimilates except under extreme conditions. Iri contrast, leaf dry weight, and consequently LMA, underwent large and rapid fluctuations in response to any factor that changed source and sink activities. A 60% reduction of photosynthetically active radiation involved a 24% decrease in LMA after 10 d. Carbon dioxide enrichment and fruit removal induced about a 45% and 15% increase in LMA, respectively, on plants with two fruiting trusses, but hardly affected LMA of producing plants. No significant cultivar effect could be identified. Changes in starch and soluble sugar content in leaves accounted for only 29% of diurnal variations in LMA, suggesting regular fluctuations of other components. We propose that structural LMA varies between a maximum and a minimum value according to the ratio of assimilate supply and demand during leaf development. Leaf area is independent of the supply of assimilates when the minimum structural LMA is realised. When the maximum structural LMA is attained, a storage pool of assimilates may accumulate in leaves during periods of high supply and low demand. We present a model including these hypotheses, which predicts structural and non- structural LMA variations of plants with different source-sink ratios. (C) 1998 Annals of Botany Company.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CROP, LEAVES, PHOTOSYNTHESIS, SOURCE-SINK RELATIONSHIPS

210

Bertin, N., and E. Heuvelink. 1993. Dry-matter production in a tomato crop - comparison of 2 simulation-models. *Journal of Horticultural Science* 68(6):995-1011.

TOMSIM(1.0) and TOMGRO(1.0) are two dynamic models for tomato growth and development. Their submodels for dry matter production are compared and discussed. In TOMSIM(1.0), dry matter production is simulated by a modified version of SUCROS87 (Spitters et al., 1989). Single leaf photosynthesis rates are calculated separately for shaded and sunlit leaf area at different depths in the canopy, according to the direct and diffuse components of light; daily crop gross assimilation rate (A) is computed by integration of these rates over the different depths and over the day. In TOMSIM(1.0) leaf photochemical efficiency (epsilon) and potential leaf gross photosynthesis rate at saturating light level (P(g,max)) both depend on temperature and CO₂ level. In TOMGRO(1.0) crop gross photosynthesis rate is calculated by the equation of Acock et al. (1978); epsilon is a constant and P(g,max) is a linear function of CO₂. In both models leaf photosynthesis characteristics are assumed to be identical in the whole canopy. Maintenance respiration (R(m)) and conversion efficiency (C(f)) are taken into account in the same way, except that root maintenance respiration is neglected in TOMGRO(1.0). For both models a sensitivity analysis was performed on the input variables (light intensity, temperature, CO₂ and leaf area index (LAI)) and on some of the model parameters. Under most conditions considered, simulated A was found to be 5-30% higher in TOMSIM(1.0) than in TOMGRO(1.0). At

temperatures above 18-degrees-C R(m) was also higher in TOMSIM(1.0), and C(f) was 4% higher in TOMGRO(1.0). The two models were very sensitive to changes in epsilon and to a lesser extent to changes in the light extinction coefficient, whereas the scattering coefficient of leaves had hardly any effect on the simulated A. TOMGRO(1.0) appeared to be rather sensitive to the CO₂ use efficiency, whereas at ambient CO₂ level mesophyll resistance was quite important in TOMSIM(1.0). Four sets of experimental data (differences in cultivar, CO₂ enrichment and planting date) from Wageningen (The Netherlands) and Montfavet (southern France) were used to validate the models. Average 24 h temperature and average daily CO₂ concentration values were used as input to the models. For the Wageningen experiments, hourly PAR values were calculated from the daily global radiation sum by TOMSIM(1.0) and used as input in both models. For the Montfavet experiment, average hourly PAR measurements were used. Also measured LAI, dry matter distribution and organ dry weights (for calculation of R(m)) were input to the simulation. In the Wageningen experiments, total dry matter production was simulated reasonably well by both models, whereas in the Montfavet experiment an under- estimation of about 35% occurred. TOMGRO(1.0) and TOMSIM(1.0) simulated almost identical curves in all four experiments. Strong and weak points of both models are discussed.

KEYWORDS: CANOPY, CO₂, GAS-EXCHANGE, GROWTH, LEAVES, LIGHT, PHOTOSYNTHESIS, YIELD

211

Bertoni, G.P., and W.M. Becker. 1996. Expression of the cucumber hydroxypyruvate reductase gene is down-regulated by elevated CO₂. *Plant Physiology* 112(2):599-605.

We examined the effects of CO₂ concentration on the white- light-stimulated expression of the cucumber (*Cucumis sativus* L.) Hpr gene. Hpr encodes hydroxypyruvate reductase, an enzyme important in the photorespiratory glycolate pathway, which plays an integral role in carbon allocation in C-3 plants. Because CO₂ is an end product of this pathway and because increased CO₂ concentrations lessen the need for photorespiration, we tested whether exposure of plants to elevated CO₂ would affect white-light-stimulated Hpr gene expression. Exposure of dark-adapted cucumber seedlings to elevated CO₂ (2 to 3 times ambient) during a 4-h white-light irradiation significantly inhibited the accumulation of Hpr mRNA. Increasing the CO₂ concentration during irradiation to 6 or 9 times ambient did not further inhibit Hpr mRNA accumulation. The depressing effect of high CO₂ on Hpr mRNA accumulation was seen in both high and low light, but was more pronounced in higher light. These results suggest that maximum sensitivity to CO₂ occurs in conditions near those normally encountered by the plant (high light, CO₂ concentration near ambient) and support a model in which white-light-regulated Hpr expression is modulated in part by environmental CO₂ concentration.

KEYWORDS: COTYLEDONS, PHOTORESPIRATION, PLANT, SEQUENCE

212

Besford, R.T. 1993. Photosynthetic acclimation in tomato plants grown in high co₂. *Vegetatio* 104:441-448.

The effects of prolonged CO₂ enrichment of tomato plants on photosynthetic performance and Calvin cycle enzymes, including the amount and activity of ribulose-1,5-bisphosphate carboxylase (RuBPco), were determined. Also the light-saturated rate of photosynthesis (P(max)) of the 5th leaf throughout leaf development was predicted based on the amount and kinetics of RuBPco. With short-term CO₂ enrichment, i.e. only during the photosynthesis measurements, P(max) of the young leaves did not increase while the leaves reaching full

expansion more than doubled their net rate of CO₂ fixation. However, with longer-term CO₂ enrichment, i.e. growing the crop in high CO₂, the plants did not maintain this photosynthetic gain. Compared with leaves of plants grown in normal ambient CO₂ the high CO₂-grown leaves, when almost fully expanded, contained only about half as much RuBPCo protein and P(max) in 300 and 1000 vpm CO₂ was similarly reduced. The loss of RuBPCo protein may be a factor associated with the accelerated fall in P(max) since P(max) was close to that predicted from the amount and kinetics of RuBPCo assuming RuBP saturation. Acclimation to high CO₂ is fundamentally different from acclimation to high light. In contrast to acclimation to high light, acclimation to high CO₂ does not usually involve an increase in photosynthetic machinery so the synthesis and maintenance costs (as indicated by the dark respiration rate) are generally lower.

KEYWORDS: ACTIVATION, CALVIN CYCLE ENZYMES, ENRICHMENT, HIGH ATMOSPHERIC CO₂, LEAVES, NITROGEN, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RICE, WHEAT

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Betsche, T. 1994. Atmospheric CO₂ enrichment - kinetics of chlorophyll a fluorescence and photosynthetic CO₂ uptake in individual, attached cotton leaves. *Environmental and Experimental Botany* 34(1):75-86.

Chl fluorescence and gas exchange of attached cotton leaves (*Gossypium hirsutum* L.) were measured in ambient air and in a highly CO₂-enriched atmosphere (4000 $\mu\text{mol mol}^{-1}$ CO₂; photosynthetic saturation). In the short term (hours to one day), net CO₂ uptake approximately doubled in all leaves examined. Photochemical (q(P)) and nonphotochemical (q(NP)) quenching of chlorophyll fluorescence, and calculated linear photosynthetic electron flow, did not change significantly when CO₂ rose from 250 to 4000 $\mu\text{mol mol}^{-1}$ CO₂. These results show that high CO₂ concentration did not inhibit photosynthesis in any leaf. In contrast, the long-term response of leaves to atmospheric CO₂-enrichment was variable. Some leaves sustained the initial high level of photosynthetic stimulation for more than a week while in others photosynthetic CO₂-uptake declined more or less. These leaves turned yellowish-green although chlorophyll content declined little. Variance in the degree of leaf yellowing was also encountered in experiments with clover when sets of plants were CO₂-enriched. Gas exchange and chl fluorescence results suggest that yellowing of cotton leaves in high CO₂ was not equivalent to 'natural' senescence although some chlorophyll fluorescence parameters changed similarly. During extended high CO₂ treatment the level of q(NP) increased notably in the yellowing leaves. The high levels of q(NP) and relaxation kinetics of chl fluorescence quenching recorded upon darkening demonstrate that thylakoid energization increased during the decline of photosynthetic CO₂ uptake in high CO₂. This shows that the photosynthetic decline was not caused by decreasing thylakoid energization because of physical damage by oversized starch grains. Calculated photosynthetic electron flow declined little suggesting that CO₂ at ribulosebiphosphate carboxylase-oxygenase fell and thus photorespiration rose. With regard to growth limitation in high CO₂ concentration, these results support the concept that high CO₂ concentration tends to induce low inorganic phosphate concentrations (Morin et al. *Plant Physiol.* 99, 89-95, 1992; Duchein et al. *J. Exp. Bot.* 44, 17-22, 1993) which can limit chloroplast ATP synthase and thus increase thylakoid energization. It is proposed that the different responses of individual leaves to atmospheric CO₂ enrichment reflects variety among leaves in the phosphate status or in the capacity for Pi-recycling (assimilate utilization).

KEYWORDS: CARBON DIOXIDE, CROP RESPONSES, DROUGHT STRESS, ELECTRON-TRANSPORT, ELEVATED CO₂, GROWTH, INORGANIC-PHOSPHATE, PHASEOLUS-VULGARIS L, PLANT NUTRITION, STARCH

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Bettarini, I., G. Calderoni, F. Miglietta, A. Raschi, and J. Ehleringer. 1995. Isotopic carbon discrimination and leaf nitrogen content of erica-arborea L along a CO₂ concentration gradient in a CO₂ spring in Italy. *Tree Physiology* 15(5):327-332.

We studied a Mediterranean species (*Erica arborea* L.) growing in a CO₂ spring in Italy that was naturally exposed for generations to a gradient of atmospheric CO₂ concentrations. The CO₂ concentration gradient to which different individual plants were exposed was determined by an indirect method based on radioisotope analysis. The stable carbon isotope ratio of sampled leaves was determined by mass spectrometry, and isotopic discrimination was then calculated. Leaf nitrogen, specific leaf area, total soil nitrogen, soil organic matter content and soil pH were also measured. In one group of plants, grown on a homogeneous soil and exposed to moderate CO₂ enrichment, isotopic discrimination was significantly reduced in response to increasing CO₂ concentrations, whereas the intercellular CO₂ concentration and leaf nitrogen content were almost unaffected. In a second group of plants, grown along a gradient of CO₂ concentration and soil nitrogen content, leaf nitrogen content was reduced when nitrogen availability was limiting. However, when soil nitrogen was available in excess, even very high CO₂ concentrations did not result in increased discrimination or reduced leaf nitrogen content in the long term. The results are discussed with respect to current theories about the long-term CO₂ response of plants based on several years of experimentation with elevated atmospheric CO₂ concentrations under controlled conditions.

KEYWORDS: ELEVATED CO₂, ENVIRONMENT, LEAVES, PHOTOSYNTHESIS, PLANT-RESPONSES, STOMATAL DENSITY

215

Bettarini, I., F.P. Vaccari, and F. Miglietta. 1998. Elevated CO₂ concentrations and stomatal density: observations from 17 plant species growing in a CO₂ spring in central Italy. *Global Change Biology* 4(1):17-22.

Stomatal density (SD) and stomatal conductance (g(s)) can be affected by an increase of atmospheric CO₂ concentration. This study was conducted on 17 species growing in a naturally enriched CO₂ spring and belonging to three plant communities. Stomatal conductance, stomatal density and stomatal index (SI) of plants from the spring, which were assumed to have been exposed for generations to elevated [CO₂], and of plants of the same species collected in a nearby control site, were compared. Stomatal conductance was significantly lower in most of the species collected in the CO₂ spring and this indicated that CO₂ effects on g, are not of a transitory nature but persist in the long term and through plant generations. Such a decrease was, however, not associated with changes in the anatomy of leaves: SD was unaffected in the majority of species (the decrease was only significant in three out of the 17 species examined), and also SI values did not vary between the two sites with the exception of two species that showed increased SI in plants grown in the CO₂-enriched area. These results did not support the hypothesis that long-term exposure to elevated [CO₂] may cause adaptive modification in stomatal number and in their distribution.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CONDUCTANCE, EXPOSURE, GAS-EXCHANGE, GRASSLAND, INCREASE, LEAVES, RESPONSES, TREES

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Betts, R.A., P.M. Cox, S.E. Lee, and F.I. Woodward. 1997. Contrasting physiological and structural vegetation feedbacks in climate change simulations. *Nature* 387(6635):796-799.

Anthropogenic increases in the atmospheric concentration of carbon

dioxide and other greenhouse gases are predicted to cause a warming of the global climate by modifying radiative forcing(1). Carbon dioxide concentration increases may make a further contribution to warming by inducing a physiological response of the global vegetation-a reduced stomatal conductance, which suppresses transpiration(2). Moreover, a CO₂-enriched atmosphere and the corresponding change in climate may also alter the density of vegetation cover, thus modifying the physical characteristics of the land surface to provide yet another climate feedback(3-6). But such feedbacks from changes in vegetation structure have not yet been incorporated into general circulation model predictions of future climate change. Here we use a general circulation model iteratively coupled to an equilibrium vegetation model to quantify the effects of both physiological and structural vegetation feedbacks on a doubled- CO₂ climate. On a global scale, changes in vegetation structure are found to partially offset physiological vegetation-climate feedbacks in the long term, but overall vegetation feedbacks provide significant regional-scale effects.

KEYWORDS: CANOPY, EUROPE, FOREST, IMPACT, LAND, MODEL, SENSITIVITY

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Bezemer, T.M., and T.H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂: quantitative analyses and guild effects. *Oikos* 82(2):212-222.

Interactions between insect herbivores and plants grown under conditions of ambient and elevated CO₂ were investigated by analysing data on 43 herbivores, representing 61 plant- herbivore interactions. Changes in herbivore performance in enhanced CO₂ environments were correlated with changes in the quality of the host plants, measured as nitrogen content, water content, carbohydrate content and secondary plant compounds. The data were analysed to determine whether CO₂ mediated effects on insect performance differed between feeding guilds (leaf-chewers, leaf miners, phloem-feeders (root and shoot), xylem-feeders, whole-cell-feeders and seed-eaters) or instar stage. Host-plant quality changed in elevated CO₂; leaf nitrogen content decreased, on average, by 15% while carbohydrates increased by 47% and secondary plant compounds (phenolics) by 31%. Water content did not change. Of the variables measured, changes in nitrogen and carbohydrate levels only were found to be correlated with changes in food consumption. No differences were found in CO₂-mediated herbivore responses on woody plant compared with non-woody plants. Insects from different feeding guilds respond to CO₂ mediated changes in host-plant quality in various ways. Leaf- chewers generally seem able to compensate for the decreased nitrogen levels in the plant tissues by increasing their food consumption (by 30%) and with no adverse effects on pupal weights. Leaf-miners only slightly increase their food consumption. The negative effect on pupal weight suggests that their population dynamics may change over several generations. Limited data on seed-eaters suggest that enhanced CO₂ conditions have no effect on these insects. Phloem-feeders and whole-cell-feeders are the only insects to show a positive CO₂ response. Population sizes generally increased in elevated CO₂ and development time of phloem-feeders was reduced by 17%. Early instar larvae are restricted more by CO₂ enhancement than late instars. Although changes in food consumption are similar, changes in development times are much more pronounced in young instars (18% vs 6%).

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CLIMATE CHANGE, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, NOCTUIDAE, NUTRIENT BALANCE, PAPER BIRCH, PERFORMANCE, RESPONSES

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Bezemer, T.M., T.H. Jones, and K.J. Knight. 1998. Long-term effects of elevated CO₂ and temperature on populations of the peach potato

aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. *Oecologia* 116(1-2):128-135.

Model terrestrial ecosystems were set-up in the Ecotron controlled environment facility. The effects of elevated CO₂ (ambient + 200 μmol/mol) and temperature (ambient + 2.0 degrees C) on plant chemistry, the abundance of the peach potato aphid *Myzus persicae*, and on the performance of one of its parasitoids *Aphidius matricariae*, were studied. Total above-ground plant biomass at the end of the experiment was not affected by elevated atmospheric CO₂, nor were foliar nitrogen and carbon concentrations. Elevated temperature decreased final plant biomass while leaf nitrogen concentrations increased. Aphid abundance was enhanced by both the CO₂ and temperature treatment. Parasitism rates remained unchanged in elevated CO₂, but showed an increasing trend in conditions of elevated temperature. Our results suggest that *M. persicae*, an important pest of many crops, might increase its abundance under conditions of climate change.

KEYWORDS: ATMOSPHERIC CO₂, CLIMATE CHANGE, DECOMPOSITION, DYNAMICS, ECOSYSTEMS, HERBIVORY, HOMOPTERA, INSECT PERFORMANCE, PHYTOCHEMISTRY, RESPONSES

219

Bezemer, T.M., K.J. Knight, J.E. Newington, and T.H. Jones. 1999. How general are aphid responses to elevated atmospheric CO₂? *Annals of the Entomological Society of America* 92(5):724-730.

We studied the impact of elevated CO₂ on 2 aphid pest species, *Myzus persicae* and *Brevicoryne brassicae* (Homoptera: Aphididae), on a series of host plants in 3 independent studies each differing in experimental complexity. Measurements on individual aphids showed that host plant and aphid species significantly influenced the response to elevated CO₂. These differences occurred not only in the level of responsiveness but also directionally. *B. brassicae* reared on *Brassica oleracea* produced significantly less offspring at elevated CO₂, whereas the opposite was found for *M. persicae* on the same host. No response was found for *M. persicae* on *Senecio vulgaris*. When populations of *B. brassicae* and *M. persicae* were followed for a longer period, no differences were observed in population sizes. Comparisons between different experimental systems show that long-term population responses to elevated CO₂ can not be reliably predicted from detailed measurements on individual aphids. The consequences of these findings for climate change research are discussed.

KEYWORDS: BREVICORYNE-BRASSICAE, CARBON DIOXIDE, CLIMATE CHANGE, DECIDUOUS TREES, HERBIVORE INTERACTIONS, INSECT PERFORMANCE, MYZUS-PERSICAE, PLANT, POPULATION-DYNAMICS, TERRESTRIAL ECOSYSTEMS

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Bezemer, T.M., L.J. Thompson, and T.H. Jones. 1998. *Poa annua* shows inter-generational differences in response to elevated CO₂. *Global Change Biology* 4(6):687-691.

Inter-generational effects on the growth of *Poa annua* (L.) in ambient and elevated atmospheric CO₂ conditions (350 and 550 μmol(-1), respectively) were studied in two different experiments. Both experiments showed similar results. In a greenhouse experiment growth, measured as the numbers of tillers produced per week, was compared for plants grown from first and second generation seeds. Second generation seeds were obtained from plants grown for one whole generation in either ambient or elevated atmospheric CO₂ ('ambient' and 'elevated' seeds, respectively). First generation plants and second generation 'ambient' plants did not respond to elevated CO₂. Second generation 'elevated' plants produced significantly more tillers in elevated CO₂. In

the second experiment model terrestrial ecosystems growing in the Ecotron and which included *Poa annua* were used. Above-ground biomass after one and two generations of growth were compared. At the end of Generation 1 no difference was found in biomass production while at the end of Generation 2 biomass increased in elevated CO₂ by 50%. The implications for climate change research are discussed.

KEYWORDS: ECOTRON, ENVIRONMENTS, FACILITY, GROWTH, PLANTS, POPULATION

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Bhattacharya, N.C., D.R. Hileman, P.P. Ghosh, R.L. Musser, S. Bhattacharya, and P.K. Biswas. 1990. Interaction of enriched CO₂ and water-stress on the physiology of and biomass production in sweet-potato grown in open-top chambers. *Plant, Cell and Environment* 13(9):933-940.

The objective of this study was to investigate the effects of water stress in sweet potato (*Ipomoea batatas* L. [Lam] 'Georgia Jet') on biomass production and plant-water relationships in an enriched CO₂ atmosphere. Plants were grown in pots containing sandy loam soil (Typic Paleudult) at two concentrations of elevated CO₂ and two water regimes in open-top field chambers. During the first 12 d of water stress, leaf xylem potentials were higher in plants grown in a CO₂ concentration of 438 and 666- μ mol mol⁻¹ than in plants grown at 364- μ mol mol⁻¹. The 364- μ mol mol⁻¹ CO₂ grown plants had to be rewatered 2d earlier than the high CO₂-grown plants in response to water stress. For plants grown under water stress, the yield of storage roots and root:shoot ratio were greater at high CO₂ than at 364- μ mol mol⁻¹; the increase, however, was not linear with increasing CO₂ concentrations. In well-watered plants, biomass production and storage root yield increased at elevated CO₂, and these were greater as compared to water-stressed plants grown at the same CO₂ concentration.

KEYWORDS: ATMOSPHERIC CO₂, ELEVATED CARBON-DIOXIDE, FIELD, PHOTOSYNTHESIS, SOYBEANS, YIELD

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Bhattacharya, N.C., J.W. Radin, B.A. Kimball, J.R. Mauney, G.R. Hendrey, J. Nagy, K.F. Lewin, and D.C. Ponce. 1994. Leaf water relations of cotton in a free-air CO₂-enriched environment. *Agricultural and Forest Meteorology* 70(1-4):171-182.

As part of an intensive study of crop response to CO₂ enrichment in a free-air CO₂ enrichment (FACE) experiment in the field, we determined aspects of the water relations of a cotton crop on selected dates in 1991. The atmosphere was enriched from 370 μ mol CO₂ mol⁻¹ (control) to about 550 μ mol mol⁻¹ in free air during daylight hours. Under full irrigation, CO₂ enrichment decreased stomatal conductance and single-leaf transpiration only toward the end of the season, and these changes led to increased leaf water potentials only at that time of year. Under water-stressed (deficit irrigation) conditions, CO₂ enrichment decreased conductance throughout the season but there was no corresponding consistent effect on leaf water potentials. As with the fully irrigated controls, CO₂ enrichment increased leaf water potentials only at the end of the season. CO₂ enrichment increased season-long biomass accumulation 39% under full irrigation and 34% under deficit irrigation. These results are consistent with previous studies of cotton in open-top chambers that found only small effects of CO₂ enrichment on internal water relations of cotton, and no water stress-induced increase in crop responsiveness to elevated CO₂.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO₂-ENRICHMENT, CONDUCTANCE, GROWTH, PHOSPHORUS, PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, STRESS, YIELD

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Bialczyk, J., Z. Lechowski, and A. Libik. 1998. Modification of tannin concentration by abiotic factors in *Lycopersicon esculentum* Mill. seedlings. *Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection* 105(3):264-273.

Results of the study on the effect of some abiotic factors on the modification of Leaf tannin concentration of greenhouse tomato seedlings are discussed in the work. The total content of soluble and insoluble tannins was calculated as tannic acid equivalent x g(-1) dry matter. The cultivars of tomato were characterized by the differentiated tannin content in leaves, stems; and roots, the proportion being 1 : 1/2 and 1/3, respectively. Two of the investigated cultivars were characterized by extreme values of the natural tannin content (cv. 'Baron' with the greatest content and cv. 'Perkoz' with the smallest one), the differences between them reaching about 240 %. A partial defoliation-or mechanical wounding of leaf blades increased the content of tannins in these organs, in relation to the effect of the partial defoliation (about 50 % of leaves being cut off), the content of tannins was higher in the case of pricking the leaves with needles. Depending on the number of pricks per cm² of the leaf blade (8, 20 or; 40), associated with a different degree of its wounding (1 %, 2.5 %, and 5 %, respectively), a maximum increase in tannin content was 180 % with 20 pricks x cm(-2) as compared with the control. The intensity of photosynthetically active radiation (PAR) significantly affected the kinetics of tannin synthesis. In the case of a 90 % reduction of daily PAR intensity, the content of tannins was reduced by about 50 % after a 2-week experiment with the two cultivars. Changes in CO₂ concentration in the environment of seedlings differently modified the level of leaf tannins. With CO₂ concentration reduced to 170 μ mol x mol(-1) air, the content of tannins decreased to about 76 % of the value evidenced in atmospheric air. CO₂ elevated to 680 μ mol x mol(-1) air induced an increase in leaf tannins to about 112- 121 % in relation to the control. The enrichment of soil solution with phosphorus or nitrogen compounds had different and opposing effects on tannin content. With phosphorus enrichment of the substrate, the content of tannins in leaves increased to about 120 % in relation to the control. The elevated nitrogen concentration reduced the content of tannins by about 30 % after a 2-week experiment. The results concerning the effect of abiotic factors on the tannin level in the leaves of greenhouse tomato seedlings could lead to the development of control measures based-on the activation of the natural defense system of plants against herbivores.

KEYWORDS: CARBON NUTRIENT BALANCE, CO₂, PATHWAY, PHYTOCHEMISTRY, POLYPHENOL OXIDASE, RESPONSES

224

Bialczyk, J., Z. Lechowski, and A. Libik. 1999. The protective action of tannins against glasshouse whitefly in tomato seedlings. *Journal of Agricultural Science* 133:197-201.

The synthesis and accumulation of tannins on tomato seedlings are regulated by environmental factors. The variation in the content of tannins was sufficiently important to bring about the occurrence of significant differences in the numbers of glasshouse whitefly on the seedlings. During a 2-week experiment, the treatments included mechanical wounding (20 prickings per cm²), spraying with kinetin solutions of 10(-4) mol/dm³, plant growth regulators, and the atmosphere enrichment to 680 μ mol CO₂/mol air, the content of tannins being increased by c. 40, 70, 10-45 and 25 % above the values obtained in the control. These results were correlated with a decrease in the numbers of insects occurring on the seedlings by c. 35, 45, 8-29 and 18 %, respectively. Contrary to the above results the spraying with solutions of abscisic acid, gibberellic acid, and the incubation of plants in an atmosphere containing 170 μ mol CO₂/mol air, reduced the content of tannins by c. 69, 22 and 25 %, respectively. This was reflected in the respective increases by c. 70, 40 and 35% in the numbers

of insects occurring on the seedlings. The obtained results suggest that tannins seem to have a dosage-dependent effect on glasshouse whitefly. Decreasing the host plant quality by increasing tannin content may act as an important selective agent limiting the losses brought about by glasshouse whitefly in tomato cultivation.

KEYWORDS: CHEMICAL DEFENSE, CO₂, GROWTH, METABOLISM, NUTRIENT, PLANT POLYPHENOLS, RESPONSES, TREE

225

Billes, G., H. Rouhier, and P. Bottner. 1993. Modifications of the carbon and nitrogen allocations in the plant (*triticum-aestivum* L) soil system in response to increased atmospheric CO₂ concentration. *Plant and Soil* 157(2):215-225.

The aim of this work was to examine the response of wheat plants to a doubling of the atmospheric CO₂ concentration on: (1) carbon and nitrogen partitioning in the plant, (2) carbon release by the roots; and (3) the subsequent N uptake by the plants. The experiment was performed in controlled laboratory conditions by exposing fast-growing spring wheat plants, during 28 days, to a (CO₂)-C-14 concentration of 350 or 700 μL L⁻¹ at two levels of soil nitrogen fertilization. Doubling CO₂ availability increased total plant production by 34% for both N treatment. In the N-fertilized soil, the CO₂ enrichment resulted in an increase in dry mass production of 41% in the shoots and 23% in the roots; without N fertilization this figure was 33% and 37%, respectively. In the N-fertilized soil, the CO₂ increase enhanced the total N uptake by 14% and lowered the N concentration in the shoots by 23%. The N concentration in the roots was unchanged. In the N-fertilized soil, doubling CO₂ availability increased N uptake by 32% but did not change the N concentrations, in either shoots or roots. The CO₂ enrichment increased total root-derived carbon by 12% with N fertilization, and by 24% without N fertilization. Between 85 and 90% of the total root derived-C-14 came from respiration, leaving only 10 to 15% in the soil as organic C-14. However, when total root-derived C-14 was expressed as a function of root dry weight, these differences were only slightly significant. Thus, it appears that the enhanced carbon release from the living roots in response to increased atmospheric CO₂, is not due to a modification of the activity of the roots, but is a result of the increased size of the root system. The increase of root dry mass also resulted in a stimulation of the soil N mineralization related to the doubling atmospheric CO₂ concentration. The discussion is focused on the interactions between the carbon and nitrogen allocation, especially to the root system, and the implications for the acquisition of nutrients by plants in response to CO₂ increase.

KEYWORDS: DIOXIDE, DRY-MATTER, ELEVATED CO₂, ENRICHMENT, GROWTH, METABOLISM, MICROBIAL BIOMASS, MINERAL NUTRITION, RESPIRATION, ROOT-DERIVED MATERIAL

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Bindi, M., L. Fibbi, B. Gozzini, S. Orlandini, and F. Miglietta. 1996. Modelling the impact of future climate scenarios on yield and yield variability of grapevine. *Climate Research* 7(3):213-224.

A mechanistic growth model was used to evaluate the mean yield and yield variability of grapevine *Vitis vinifera* L. under current and future climates. The model used was previously validated using field experiment data. The effect of elevated CO₂ on grapevine growth was also considered. Adaptation of 2 varieties (Sangiovese and Cabernet Sauvignon) to scenarios of increased CO₂ and climate change, and potential changes in agricultural risk (i.e. inter-seasonal variability), were examined. Before testing the effect of climate scenarios, we analysed the sensitivity of modelled grapevine yield to arbitrary changes in the 3 driving variables (temperature, solar radiation and CO₂). The

results showed the model to be more sensitive to changes in CO₂ concentration and temperature than to changes in radiation. Analyses made using transient GCM (general circulation model) scenarios (UKTR and GFDL) showed different changes in mean fruit dry matter for the different scenarios, whereas mean total dry matter, and fruit and total dry matter variability, were predicted to increase under almost all the scenarios. Predictions based on equilibrium scenarios (UKLO and UKHI) gave similar results. For Sangiovese, variety adaptation analysis suggested a better adaptation in terms of mean production, but a worse adaptation in terms of yield variability.

KEYWORDS: CO₂, RADIATION, TEMPERATURE

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Biondi, F., and J.E. Fessenden. 1999. Response of lodgepole pine growth to CO₂ degassing at Mammoth Mountain, California. *Ecology* 80(7):2420-2426.

We conducted dendroclimatic and stable isotope analyses of lodgepole pines (*Pinus contorta*) located in high-mortality sites at Mammoth Mountain (California, USA) to test for tree responses to magmatic degassing. Existing climatic and tree-ring data from nearby Yellowstone National Park were used for comparison. Sampled trees were scarcely sensitive to climate, and their growth showed an overall decline during the 20th century. Past growth rates of currently dead and stressed pines plummeted after 1990, when degassing of magmatic CO₂ was first reported in the area. No consistent or strong correlation was found with monthly and seasonal climatic parameters. Stable carbon isotopes were measured on holocellulose extracted from annual rings of a dead pine, a stressed pine, and a live pine. The delta(13)C signature of the dead and stressed pines showed enrichment in heavy carbon beginning in 1990, which could be related to stomatal closure following impairment of root systems by high levels of magmatic CO₂ in the soil.

KEYWORDS: CARBON, EMISSION, ISOTOPE, LONG VALLEY CALDERA, RATIOS, RINGS, UNREST

228

Bishop, D.L., and B.G. Bugbee. 1998. Photosynthetic capacity and dry mass partitioning in dwarf and semi-dwarf wheat (*Triticum aestivum* L.). *Journal of Plant Physiology* 153(5-6):558-565.

Efficient use of space and high yields are critical for long-term food production aboard the International Space Station. The selection of a full dwarf wheat (less than 30 cm tall) with high photosynthetic and yield potential is a necessary prerequisite for growing wheat in the controlled, volume-limited environments available aboard long-term spaceflight missions. This study evaluated the photosynthetic capacity and carbon partitioning of a full-dwarf wheat cultivar, Super Dwarf, which is routinely used in spaceflight studies aboard U.S. space shuttle and NASA/Mir missions and made comparisons with other dwarf and semi-dwarf wheat cultivars utilized in other ground-based studies in plant space biology. Photosynthetic capacity of the flag leaf in two dwarf (Super Dwarf, BB-19), and three semi-dwarf (Veery-10, Yecora Rojo, IBWSN 199) wheat cultivars (*Triticum aestivum* L.) was assessed by measuring: net maximum photosynthetic rate, RuBP carboxylation efficiency, chlorophyll concentration and flag leaf area. Dry mass partitioning of carbohydrates to the leaves, sheaths, stems and ear was also assessed. Plants were grown under controlled environmental conditions in three replicate studies: slightly enriched CO₂ (370 μmol mol⁻¹), high photosynthetic photon flux (1000 μmol m⁻² s⁻¹); 58 μmol m⁻² d⁻¹) for a 16 h photoperiod, 22/15 degrees C day/night temperatures, ample nutrients and water provided by one-half strength Hoagland's nutrient solution (Hoagland and Amen, 1950). Photosynthetic capacity of the flag leaf was determined at anthesis using net CO₂ exchange rate versus internal CO₂ concentration curves

measured under saturating light (2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and CO_2 (1000 $\mu\text{mol mol}^{-1}$). Dwarf wheat cultivars had greater photosynthetic capacities than the taller semi-dwarfs, they averaged 20 % higher maximum net photosynthetic rates compared to the taller semi-dwarfs, but these higher rates occurred only at anthesis, had slightly greater carboxylation efficiencies and significantly increased chlorophyll concentrations per unit leaf area. The reduced-height wheat had significantly less dry mass fraction in the stem but greater dry mass partitioned to the ear than the taller semi-dwarfs (Yecora rojo, IBWSN-199). Studies with detached heads confirm that the head is a significant sink in the shorter wheat cultivars.

KEYWORDS: BIOCHEMISTRY, CANOPY, FLAG LEAF, GAS-EXCHANGE, HEIGHT, LEAVES, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE, SPRING WHEAT, SUCROSE METABOLISM, WINTER-WHEAT

229

Biswas, P.K., D.R. Hileman, P.P. Ghosh, N.C. Bhattacharya, and J.N. McCrimmon. 1996. Growth and yield responses of field-grown sweetpotato to elevated carbon dioxide. *Crop Science* 36(5):1234-1239.

Root crops are important in developing countries, where food supplies are frequently marginal. Increases in atmospheric CO_2 usually lead to increases in plant growth and yield, but little is known about the response of root crops to CO_2 enrichment under field conditions. This experiment was conducted to investigate the effects of CO_2 enrichment on growth and yield of field-grown sweetpotato [*Ipomoea batatas* (L.) Lam.]. Plants were grown in open-top chambers in the field at four CO_2 levels ranging from 354 (ambient) to 665 $\mu\text{mol mol}^{-1}$ in two growing seasons. Shoot growth was not affected significantly by elevated CO_2 . Yield of storage roots increased 46 and 75% at the highest CO_2 level in the 2 yr. The yield enhancement occurred through increases in the number of storage roots in the first year and through increases in both the number and size of the storage roots in the second year. Storage-root/shoot ratios increased 44% and leaf nitrogen concentrations decreased by 24% at the highest CO_2 level. A comparison of plants grown in the open field to plants grown in open-top chambers at ambient CO_2 concentrations indicated that open-top chambers reduced shoot growth in the first year and storage-root yield in both years. These results are consistent with the majority of CO_2 -enrichment studies done on pot-grown sweetpotato.

KEYWORDS: ATMOSPHERIC CO_2 ENRICHMENT, COTTON, ENVIRONMENT, IRRIGATION, NITROGEN, OPEN-TOP CHAMBERS, PHYSIOLOGY, PLANT-RESPONSES, SWEET-POTATO, WATER-STRESS

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Bjorn, L.O., T.V. Callaghan, I. Johnsen, J.A. Lee, Y. Manetas, N.D. Paul, M. Sonesson, A.R. Wellburn, D. Coops, H.S. Heide-Jorgensen, C. Gehrke, D. Gwynn-Jones, U. Johanson, A. Kyparissis, E. Levizou, D. Nikolopoulos, Y. Petropoulou, and M. Stephanou. 1997. The effects of UV-B radiation on European heathland species. *Plant Ecology* 128(1-2):252-264.

The effects of enhanced UV-B radiation on three examples of European shrub-dominated vegetation were studied in situ. The experiments were in High Arctic Greenland, northern Sweden and Greece, and at all sites investigated the interaction of enhanced UV-B radiation (simulating a 15% reduction in the ozone layer) with artificially increased precipitation. The Swedish experiment also involved a study of the interaction between enhanced UV-B radiation and elevated CO_2 (600 ppm). These field studies were supported by an outdoor controlled environment study in the United Kingdom involving modulated enhancement of UV-B radiation in combination with elevated CO_2 (700

ppm). Effects of the treatments on plant growth, morphology, phenology and physiology were measured. The effects observed were species specific, and included both positive and negative responses to the treatments. In general the negative responses to UV-B treatments of up to three growing seasons were small, but included reductions in shoot growth and premature leaf senescence. Positive responses included a marked increase in flowering in some species and a stimulation of some photosynthetic processes. UV-B treatment enhanced the drought tolerance of *Pinus pinea* and *Pinus halepensis* by increasing leaf cuticle thickness. In general, there were few interactions between the elevated CO_2 and enhanced UV-B treatments. There was evidence to suggest that although the negative responses to the treatments were small, damage may be increasing with time in some long-lived woody perennials. There was also evidence in the third year of treatments for effects of UV-B on insect herbivory in *Vaccinium* species. The experiments point to the necessity for long-term field investigations to predict the likely ecological consequences of increasing UV-B radiation.

KEYWORDS: ACTION SPECTRA, DROUGHT, FIELD CONDITIONS, GROWTH, LEAVES, PHOTOSYNTHESIS, SOLAR ULTRAVIOLET-RADIATION, STOMATAL CLOSURE, SURFACE, TERRESTRIAL PLANTS

231

Bladier, C., and P. Chagvardieff. 1993. Growth and photosynthesis of photoautotrophic callus derived from protoplasts of *Solanum tuberosum* L. *Plant Cell Reports* 12(6):307-311.

We describe a photoautotrophic culture procedure of potato (cvs Kennebec, Haig, DTO-33) callus derived from mesophyll protoplasts. The protoplast culture was initiated at very low concentration of glucose (down to 0.25 g l⁻¹). Callus was subcultured under CO_2 enriched air and glucose was suppressed by the successive dilutions with glucose free media. Regeneration was successfully obtained under photoautotrophic conditions. The characterization of oxygen exchange and of some enzymes and metabolites of carbon assimilation indicated that chlorophyllous callus, grown on carbohydrate free medium, developed the photosynthetic pathway typical of C3 plants. By comparing the fresh weight of callus cultivated in the light or in non-photosynthetic conditions (in darkness or in the light +3-(3,4-Dichlorophenyl)-1,1-dimethylurea) we concluded that growth depended to about 70 to 88 % on photosynthesis.

KEYWORDS: CELL-SUSPENSION CULTURES, CO_2 , LIGHT, METABOLISM, MUTANTS, NICOTIANA-PLUMBAGINIFOLIA, OXYGEN- EXCHANGE, PLANTS, RESPIRATION, SUCROSE

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Blobner, M., R. Bogdanski, E. Kochs, J. Henke, A. Findeis, and S. Jelen-Esselborn. 1998. Effects of intraabdominally insufflated carbon dioxide and elevated intraabdominal pressure on splanchnic circulation - An experimental study in pigs. *Anesthesiology* 89(2):475-482.

Background Intraabdominally insufflated carbon dioxide (CO_2) during laparoscopy may have a specific effect on splanchnic circulation that may be unrelated to the effects of increased intraabdominal pressure alone. Therefore, the influences of insufflation with CO_2 versus air on splanchnic circulation were compared. Methods: Pigs were chronically instrumented for continuous recording of mesenteric artery, portal venous, inferior vena cava, and pulmonary arterial blood flow and portal venous pressure. After induction of anesthesia, CO_2 or air was insufflated in 14 and 10 pigs, respectively. With the pigs in the supine position, intraabdominal pressure was increased in steps of 4 mmHg up to 24 mmHg by graded gas insufflation. Results: During air insufflation, mesenteric artery vascular resistance was unchanged, whereas mesenteric arterial blood flow decreased with increasing intraabdominal

pressure. Shortly after CO₂ insufflation to an intraabdominal pressure of 4 mmHg, mean arterial pressure, mesenteric arterial blood flow, and mesenteric arterial vascular resistance were increased by 21%, 12% and 9%, respectively. Subsequently, with the onset of CO₂ resorption in the third minute, mean arterial pressure declined to baseline values and mesenteric arterial vascular resistance declined to 85% of baseline values, whereas mesenteric arterial blood flow continued to increase to a maximum of 24% higher than baseline values. At steady-state conditions during CO₂ insufflation, mesenteric arterial blood flow was increased up to an intraabdominal pressure less than or equal to 16 mmHg but decreased at higher intraabdominal pressures. Conclusions: in contrast to air insufflation, intraabdominal insufflation of CO₂ resulted in a moderate splanchnic hyperemia at an intraabdominal pressure less than or equal to 12 mmHg. At higher intraabdominal pressure values, pressure-induced changes became more important than the type of gas used.

KEYWORDS: BLOOD-FLOW, DOGS, HALOTHANE ANESTHESIA, INTRA-ABDOMINAL PRESSURE, LAPAROSCOPIC CHOLECYSTECTOMY, PNEUMOPERITONEUM, RESPONSES, TENSION, VASOPRESSIN RELEASE

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Blum, H., G. Hendrey, and J. Nosberger. 1997. Effects of elevated CO₂, N fertilization, and cutting regime on the production and quality of *Lolium perenne* L. shoot necromass. *Acta Oecologica-International Journal of Ecology* 18(3):291-295.

In the Swiss grassland FACE experiment, we measured the effect of elevated CO₂ on the shoot necromass production and quality of *Lolium perenne* in 1995. Dead stubble of reproductive tillers and dead leaf sheaths were the main components of necromass. Elevated CO₂ did not significantly change the amount and the nitrogen concentration of necromass. Significantly more necromass was produced and the N concentration was lower in the low N supply treatments. Total necromass amounted to 250-500 g m⁻². Necromass N content was in the order of 5-6 g m⁻². This underscores the importance of the carbon and nitrogen fluxes included in necromass and their importance for soil biology and fertility.

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Blumenthal, C., H.M. Rawson, E. McKenzie, P.W. Gras, E.W.R. Barlow, and C.W. Wrigley. 1996. Changes in wheat grain quality due to doubling the level of atmospheric CO₂. *Cereal Chemistry* 73(6):762-766.

Elevated levels of atmospheric CO₂ have been shown to increase grain yield and reduce grain nitrogen concentration. The object of this study was to determine whether elevated CO₂ levels would modify other aspects of grain quality relevant to processing, particularly protein and starch quality. Wheat of two genotypes (Hartog and Late Hartog) was grown in the field in controlled-atmosphere tunnels at either the ambient level of CO₂ (350 μ mol/L) or an elevated level (700 μ mol/L). This elevated level of CO₂ produced significant increases in grain yield, but decreases in 1,000-kernel weight. Grain grown in the elevated CO₂ atmosphere produced poorer dough and decreased loaf volume, farinograph development time, and dough extensibility. These changes were largely attributable to the lower protein content of the grain grown at elevated CO₂. There did not appear to be major changes in protein composition or in the functional properties of the protein. Grain produced at elevated CO₂ yielded starch with a significantly higher proportion of large (A-type) starch granules but no overall change in amylose-to-amylopectin ratio. These studies indicate that elevated levels of CO₂ may result in decreased quality of bread wheats largely due to lowered protein content.

KEYWORDS: CARBON DIOXIDE, CLIMATE, GENOTYPES, GROWTH, NITROGEN APPLICATION, NUTRITION, SPRING WHEAT, TEMPERATURE, YIELD

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Boerner, R.E.J., and J. Rebbeck. 1995. Decomposition and nitrogen release from leaves of 3 hardwood species grown under elevated O₃ and/or CO₂. *Plant and Soil* 170(1):149-157.

Elevated concentrations of O₃ and CO₂ have both been shown to affect structure, nutrient status, and deposition of secondary metabolites in leaves of forest trees. While such studies have produced robust models of the effects of such air pollutants on tree ecophysiology and growth, few have considered the potential for broader, ecosystem-level effects after these chemically and structurally altered leaves fall as leaf litter and decay. To determine the effects of elevated O₃ and/or CO₂ on the subsequent decomposition and nutrient release from the leaves grown in such altered atmospheres, we grew seedlings of three widespread North American forest trees, black cherry (*Prunus serotina*) (BC), sugar maple (*Acer saccharum*) (SM), and yellow-poplar (*Liriodendron tulipifera*) (YP) for two growing seasons in charcoal-filtered air (CF-air—approximately 25% ambient O₃), ambient O₃ (1X) or twice-ambient O₃ (2X) in outdoor open-top chambers. We then assayed the loss of mass and N from the litter derived from those seedlings through one year litterbag incubations in the forest floor of a neighboring forest stand. Mass loss followed linear functions and was not affected by the O₃ regime in which the leaves were grown. Instantaneous decay rates (i.e. k values) averaged SM:-0.707 y⁻¹, BC:-0.613 y⁻¹, and YP:-0.859 y⁻¹. N loss from ambient (1X) O₃-grown SM leaves was significantly greater than from CF-air leaves; N loss from BC leaves did not differ among treatments. Significantly less N was released from CF-air-grown YP leaves than from 1X or 2X O₃-treated leaves. YP leaves from plants grown in pots at 2X O₃ and 350 ppm supplemental CO₂ in indoor pollutant fumigation chambers (CSTRs or Continuously Stirred Tank Reactors) lost 40% as much mass and 27% as much N over one year as did leaves from YP grown in CF-air or 2X O₃. Thus, for leaves from plants grown in pots in controlled environment fumigation chambers, the concentrations of both O₃ and CO₂ can affect N release from litter incubated in the field whereas mass loss rate was affected only by CO₂. Because both mass loss and N release from leaves grown at elevated CO₂ were reduced significantly (at least for yellow-poplar), forests exposed to elevated CO₂ may have significantly reduced N turnover rates, thereby resulting in increased N limitation of tree growth, especially in forests which are already N-limited.

KEYWORDS: ACIDIC RAIN, ATMOSPHERIC CO₂, CARBON DIOXIDE, OZONE, PHOTOSYNTHESIS, QUALITY, RESPONSES, SEEDLINGS, SULFUR-DIOXIDE, TREE

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Boese, S.R., and D.W. Wolfe. 1995. Elevated-temperatures limit sink development and photosynthetic benefit from elevated CO₂. *Plant Physiology* 108(2):26.

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Boese, S.R., D.W. Wolfe, and J.J. Melkonian. 1997. Elevated CO₂ mitigates chilling-induced water stress and photosynthetic reduction during chilling. *Plant, Cell and Environment* 20(5):625-632.

Bean, cucumber and corn plants were grown in controlled- environment chambers at 25/18 degrees C day/night temperature and either ambient (350 μ mol mol⁻¹) or elevated (700 μ mol mol⁻¹) CO₂ concentration, and at 20-30 d after emergence they were exposed to a 24 h chilling treatment (6.5 +/- 1.5 degrees C) at their growth CO₂

concentration. Whole-plant transpiration rates (per unit leaf area basis) during the first 3 h of chilling were about 26, 28 and 13% lower at elevated than at ambient CO₂ for bean, cucumber and corn, respectively. The decline in leaf water potential (Psi(L)) and visible wilting of bean and cucumber during chilling were significantly less at elevated than at ambient CO₂. Corn Psi(L) was not significantly affected by chilling, and corn did not exhibit any other symptoms of chilling-induced water stress. Leaf osmotic potentials (measured before chilling only) of bean and cucumber were more negative at elevated than at ambient CO₂, and the corresponding calculated leaf turgor potentials were significantly higher at elevated than at ambient CO₂. Leaf relative water content (RWC) during chilling at ambient CO₂ fell to 62 and 48% for bean and cucumber, respectively, RWC during chilling at elevated CO₂ was never below 79% for bean or 63% for cucumber. Corn RWC was not measured. After 24 h of chilling at ambient CO₂, net photosynthetic rate (PN) reductions were 83, 89 and 24% for bean, cucumber and corn, respectively. P-N reductions during chilling were less at elevated CO₂: 53, 40 and 4% for bean, cucumber and corn, respectively. At ambient CO₂, none of the species fully recovered to pre-chilling P-N, but at elevated CO₂ both bean and corn recovered fully. The average percentage leaf area with visible leaf damage due to chilling was 20.6 and 9.6% at ambient and elevated CO₂, respectively, for bean, and 32.4 and 23.6% at ambient and elevated CO₂, respectively, for cucumber. Corn showed no significant permanent leaf damage from chilling at either CO₂ concentration. These results indicate that cucumber was most sensitive to chilling as imposed in this study, followed by bean and corn. The results support the hypothesis that, at least in young plants under controlled-environment conditions, elevated CO₂ improves plant water relations during chilling and can mitigate photosynthetic depression and chilling damage. The implications for long-term growth and reproductive success in managed and natural ecosystems will require testing of this hypothesis under field conditions.

KEYWORDS: *ABSCISIC-ACID, LEAF GAS-EXCHANGE, LIGHT, LOW-TEMPERATURE, PHASEOLUS-VULGARIS L, PHOTOINHIBITION, PISUM SATIVUM L, SENSITIVE PLANTS, STOMATAL BEHAVIOR, ZEA-MAYS*

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Boetsch, J., J. Chin, M. Ling, and J. Croxdale. 1996. Elevated carbon dioxide affects the patterning of subsidiary cells in *Tradescantia* stomatal complexes. *Journal of Experimental Botany* 47(300):925-931.

The influence of elevated CO₂ concentration (670 ppm) on the structure, distribution, and patterning of stomata in *Tradescantia* leaves was studied by making comparisons with plants grown at ambient CO₂. Extra subsidiary cells, beyond the normal complement of four per stoma, were associated with nearly half the stomatal complexes on leaves grown in elevated CO₂. The extra cells shared characteristics, such as pigmentation and expansion, with the typical subsidiary cells. The position and shape of the extra subsidiary cells in face view differed in the green and purple varieties of *Tradescantia*. Substomatal cavities of complexes with extra subsidiary cells appeared larger than those found in control leaves. Stomatal frequency expressed on the basis of leaf area did not differ from the control. Stomatal frequency based on cell counts (stomatal index) was greater in leaves grown in CO₂-enriched air when all subsidiary cells were counted as part of the stomatal complex. This difference was eliminated when subsidiary cells were included in the count of epidermal cells, thereby evaluating the frequency of guard cell pairs. The extra subsidiary cells were, therefore, recruited from the epidermal cell population during development. Stomatal frequency in plants grown at elevated temperature (29 degrees C) was not significantly different from that of the control (24 degrees C). The linear aggregations of stomata were similar in plants grown in ambient and elevated CO₂. Since enriched CO₂ had no effect on the structure or patterning of guard cells, but resulted in the formation of additional subsidiary cells, it is likely that separate and independent events pattern

the two cell types. Plants grown at enriched CO₂ levels had significantly greater internode lengths, but leaf area and the time interval between the appearance of successive leaves were similar to that of control plants. Porometric measurements revealed that stomatal conductance of plants grown under elevated CO₂ was lower than that of control leaves and those grown at elevated temperature. *Tradescantia* was capable of regulating stomatal conductance in response to elevated CO₂ without changing the relative number of stomata present on the leaf.

KEYWORDS: *ARABIDOPSIS, CO₂-ENRICHMENT, DIFFERENTIATION, LEAF DEVELOPMENT, MORPHOLOGY, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS*

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Bolin, B. 1999. Effect on the biosphere of elevated atmospheric CO₂ (pg 1851). *Science* 286(5440):684.

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Bolin, B., J. Canadell, B. Moore, I. Noble, and W. Steffen. 1999. Effect on the biosphere of elevated atmospheric CO₂. *Science* 285(5435):1851-1852.

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Bolker, B.M., S.W. Pacala, F.A. Bazzaz, C.D. Canham, and S.A. Levin. 1995. Species-diversity and ecosystem response to carbon-dioxide fertilization - conclusions from a temperate forest model. *Global Change Biology* 1(5):373-381.

This paper explores how the response of a temperate forest ecosystem to climate change might depend on species diversity and community change. In particular, we look at the dynamics of a model of temperate forest growth under doubled CO₂. We combine a detailed, field-calibrated model of forest dynamics (Pacala et al. 1993) with greenhouse data on the range of seedling biomass growth response to doubled CO₂ concentrations (Bazzaz et al. 1990; Bazzaz & Miao 1993). Because total ecosystem response to climate change depends delicately on many environmental variables other than CO₂, we isolate the effects of community change by comparing runs of the regular model, allowing dynamic community change, with runs of a reduced model that holds species composition static by using a single tree species with average parameters. Simulations that allowed community change instead of holding species composition constant showed a roughly 30% additional increase in total basal area over time scales of 50-150 years. Although the model omits many possible feedbacks and mechanisms associated with climate change, it suggests the large potential effects that species differences and feedbacks can have in ecosystem models and reinforces the possible importance of diversity to ecosystem function (Naeem et al. 1994; Tilman & Downing 1994) over time scales within the planning horizon for global change policy.

KEYWORDS: *ATMOSPHERIC CO₂, CANOPY, CO₂-INDUCED CLIMATE CHANGE, ENRICHMENT, GROWTH, LIGHT, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, STORAGE, TERRESTRIAL ECOSYSTEMS*

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Bonghi, C., A. Ramina, B. Ruperti, R. Vidrih, and P. Tonutti. 1999. Peach fruit ripening and quality in relation to picking time, and hypoxic and high CO₂ short-term postharvest treatments. *Postharvest Biology and Technology* 16(3):213-222.

Peach fruits (*Prunus persica* L. Batsch, cv Springercrest) were harvested at two ripening stages (flesh firmness of 60 N, first harvest, and 45 N, second harvest) and maintained at 20 degrees C in air (control) or for 24 and 48 h in streams of ultra low (<1%) oxygen (ULO) or high (30%) CO₂ concentration and then transferred to air for up to 8 days. The decline in flesh firmness was strongly reduced by ULO and CO₂ treatments in fruits of both harvests, although the effect was stronger in fruits picked earlier in which ethylene biosynthesis remained at the basal level. In fruits of the second harvest, endo beta-1,4-glucoanase (EGase) activity was lower in ULO- and CO₂- treated fruits than in control fruits at the end of the 24 h treatment and the following two days in air. Acetaldehyde (AA) gradually accumulated in control fruit and the highest concentrations were detected during late ripening. Both treatments induced a strong accumulation of AA but, with the exception of the 24 and 48 h CO₂ treatments performed on fruits of the second harvest, a decrease in AA content was observed when the fruits were transferred to air. A slight increase in ethanol (EtOH) was found throughout the ripening process in control fruits; ULO and CO₂ strongly stimulated EtOH production. When fruits were transferred to air, EtOH concentration declined rapidly. Alcohol dehydrogenase (ADH) activity significantly increased in control fruit only in the late stages of ripening. Greater ADH activity was found throughout the experimental period in fruits of the first harvest treated for 24 h in ULO and CO₂, whereas, at day 8, control and treated fruits of the second harvest showed similar ADH activity values. Hypoxic and, to a lesser extent, CO₂- enriched atmospheres stimulated Adh gene expression. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ETHYLENE, EXPRESSION, LOW-OXYGEN ATMOSPHERES, NECTARINES, RESPONSES, STORAGE

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Booker, F.L. 1997. Effects of elevated CO₂ and nitrogen on proanthocyanidins in cotton. *Plant Physiology* 114(3):489.

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Booker, F.L., C.D. Reid, S. BrunschonHarti, E.L. Fiscus, and J.E. Miller. 1997. Photosynthesis and photorespiration in soybean [Glycine max (L.) Merr.] chronically exposed to elevated carbon dioxide and ozone. *Journal of Experimental Botany* 48(315):1843-1852.

The effects of elevated carbon dioxide (CO₂) and ozone (O₃) on soybean [Glycine max (L.) Merr.] photosynthesis and photorespiration-related parameters were determined periodically during the growing season by measurements of gas exchange, photorespiratory enzyme activities and amino acid levels. Plants were treated in open-top field chambers from emergence to harvest maturity with seasonal mean concentrations of either 364 or 726 $\mu\text{mol mol}^{-1}$ CO₂ in combination with either 19 or 13 nmol mol^{-1} O₃ (12 h daily averages). On average at growth CO₂ concentrations, net photosynthesis (A) increased 56% and photorespiration decreased 36% in terminal mainstem leaves with CO₂-enrichment. Net photosynthesis and photorespiration were suppressed 30% and 41%, respectively, by elevated O₃ during late reproductive growth in the ambient CO₂ treatment, but not in the elevated CO₂ treatment. The ratio of photorespiration to A at growth CO₂ was decreased 61% by elevated CO₂. There was no statistically significant effect of elevated O₃ in the ratio of photorespiration to A. Activities of glycolate oxidase, hydroxypyruvate reductase and catalase were decreased 10-25% by elevated CO₂, and by 46-66% by elevated O₃ at late reproductive growth. The treatments had no significant effect on total amino acid or glycine levels, although serine concentration was lower in the elevated CO₂ and O₃ treatments at several sampling dates. The inhibitory effects of elevated O₃ on photorespiration-related parameters were generally commensurate with the O₃-induced decline in A. The results suggest that elevated CO₂ could promote productivity

both through increased photoassimilation and suppressed photorespiration.

KEYWORDS: ARABIDOPSIS-THALIANA, ATMOSPHERIC CO₂, CARBOXYLASE ACTIVITY, GAS-EXCHANGE, L LEAVES, PHASEOLUS-VULGARIS L, PLANT-RESPONSES, SPRING WHEAT, SUPEROXIDE-DISMUTASE, ULTRAVIOLET-B

245

Boone, R.D., K.J. Nadelhoffer, J.D. Canary, and J.P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396(6711):570-572.

The temperature sensitivity of soil respiration will largely determine the effects of a warmer world on net carbon flux from soils to the atmosphere. CO₂ flux from soils to the atmosphere is estimated to be 50-70 petagrams of carbon per year and makes up 20-38% of annual inputs of carbon (in the form of CO₂) to the atmosphere from terrestrial and marine sources(1,2). Here we show that, for a mixed temperate forest, respiration by roots plus oxidation of rhizosphere carbon, which together produce a large portion of total effluxed soil CO₂, is more temperature-sensitive than the respiration of bulk soil. We determine that the Q(10) value (the coefficient for the exponential relationship between soil respiration and temperature, multiplied by ten) is 4.6 for autotrophic root respiration plus rhizosphere decomposition, 2.5 for respiration by soil lacking roots and 3.5 for respiration by bulk soil. If plants in a higher-CO₂ atmosphere increase their allocation of photosynthate to roots(3-6), these findings suggest that soil respiration should be more sensitive to elevated temperatures, thus limiting carbon sequestration by soils.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CO₂, EXCHANGE, FLUXES, FOREST, LITTER, VEGETATION

246

Boote, K.J., and N.B. Pickering. 1994. Modeling photosynthesis of row crop canopies. *Hortscience* 29(12):1423-1434.

KEYWORDS: CARBON DIOXIDE, CARBOXYLASE-OXYGENASE, CO₂/O₂ SPECIFICITY, DIRECT COMPONENT, ELEVATED CO₂, GLOBAL RADIATION, LEAF NITROGEN, NET PHOTOSYNTHESIS, SOYBEAN CANOPIES, USE EFFICIENCY

247

Borkhsenius, O.N., C.B. Mason, and J.V. Moroney. 1998. The intracellular localization of ribulose-1,5-bisphosphate carboxylase/oxygenase in *Chlamydomonas reinhardtii*. *Plant Physiology* 116(4):1585-1591.

The pyrenoid is a proteinaceous structure found in the chloroplast of most unicellular algae. Various studies indicate that ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is present in the pyrenoid, although the fraction of Rubisco localized there remains controversial. Estimates of the amount of Rubisco in the pyrenoid of *Chlamydomonas reinhardtii* range from 5% to nearly 100%. Using immunolocalization, the amount of Rubisco localized to the pyrenoid or to the chloroplast stroma was estimated for *C. reinhardtii* cells grown under different conditions. It was observed that the amount of Rubisco in the pyrenoid varied with growth condition; about 40% was in the pyrenoid when the cells were grown under elevated CO₂ and about 90% with ambient CO₂. In addition, it is likely that pyrenoidal Rubisco is active in CO₂ fixation because in vitro activity measurements showed that most of the Rubisco must be active to account for CO₂-fixation rates observed in whole cells. These results are consistent with the idea that the pyrenoid is the site of CO₂ fixation in *C. reinhardtii* and other unicellular algae containing CO₂-concentrating mechanisms.

KEYWORDS: CARBONIC-ANHYDRASE, CHLOROPLAST, MECHANISM, OXYGENASE, PHOTOSYNTHESIS

248

Borodin, V.B. 1995. Photosynthetic O₂ exchange in chlorella cells adapted to low CO₂ concentration under blue or red-light. *Russian Journal of Plant Physiology* 42(1):31-36.

The effect of light quality on the adaptation to low atmospheric CO₂ concentration was studied on the cells of unicellular green alga *Chlorella pyrenoidosa* 82T grown under 2% CO₂ concentration and white light. The adaptation of *Chlorella* cells was more successful under blue than under red light. Thus, the air-adapted cells under blue light showed a higher affinity for CO₂, a higher quantum efficiency of apparent photosynthesis at CO₂ limitation, and acceleration of O₂ evolution at light saturation, as compared to the red-light-adapted cells. In air-adapted cells, the photosynthetic rates at low CO₂ concentration were enhanced with increased intensities of both blue and red light, but the differences between the two treatments were retained. It was inferred that *Chlorella* cell adaptation depended on both light intensity and its spectral composition. The light intensity exerts its action via photosynthetic apparatus while spectral composition of light exerts its effect via a system of photoreception, which absorbs blue light. This additional blue light absorption is considered favorable for *Chlorella* cell adaptation to low CO₂ concentration.

KEYWORDS: ACETABULARIA-MEDITERRANEA, CARBONIC-ANHYDRASE, CHLAMYDOMONAS-REINHARDTII, INDUCTION, PROTEIN

249

Bosac, C., S.D.L. Gardner, G. Taylor, and D. Wilkins. 1995. Elevated CO₂ and hybrid poplar - a detailed investigation of root and shoot growth and physiology of *Populus deltoides* × *Populus nigra*. *Forest Ecology and Management* 74(1-3):103-116.

Exposure of the hybrid poplar clone 'Primo' (*Populus deltoides* × *Populus nigra*) to 580 μmol mol⁻¹ CO₂ for just 68 days significantly (P less than or equal to 0.05) increased stem height by 13% compared with trees grown in ambient CO₂ concentrations. The stem diameter was significantly (P less than or equal to 0.05) increased and both total biomass and woody stem biomass also showed higher values (38% and 31% increases respectively) in elevated CO₂. Trees in elevated CO₂ had more leaves and a greater total leaf area, whilst the specific leaf area was decreased in elevated CO₂ on four out of five occasions and was significantly (P less than or equal to 0.05) lower after 68 days, an effect indicating that leaves were thicker and/or heavier. Rates of photosynthesis (A) measured after 49 and 67 days of exposure revealed that trees in the elevated CO₂ treatment had lower values of A when measured at either 350 or 580 μmol mol⁻¹ CO₂. Sequential harvests at intervals during the study in which the root and shoot components were analysed separately allowed the construction of root:shoot ratios and allometric coefficients; there was no significant effect on the allometric coefficient and the root:shoot ratio was significantly increased on only one occasion. However, measurements of the 'apparent' root length suggested that root lengths were greater in the CO₂ treatment. There was a significant increase in the number of fine root tips visible down the surface of specially designed rooting tubes (P less than or equal to 0.05), indicating more fine roots or an increase in fine root branching. The growth rates of individual fine or large roots over 24 h were unaffected, again suggesting that increases in biomass may be due to more root segments rather than longer individual roots. Root water relations were also examined and showed a tendency towards solute accumulation and increases in turgor pressure (P) and effective turgor (P-e) at times when root growth was stimulated, although these were not consistent. Cell wall plasticity of the tips of large roots was significantly (P less than or equal

to 0.01) reduced in elevated CO₂, possibly indicating a greater tendency to divert resources to the formation of root branches. The results of the study are discussed in the light of the possible consequences of changes in poplar growth and physiology for forestry practice in an increased CO₂ environment.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CELL-WALLS, CLONES, CONDUCTANCE, DROUGHT, ENRICHMENT, LEAF GROWTH, PHOTOSYNTHESIS, SOURCE-SINK RELATIONS

250

Bottomley, P.A., H.H. Rogers, and S.A. Prior. 1993. Nmr imaging of root water distribution in intact vicia-faba L plants in elevated atmospheric CO₂. *Plant, Cell and Environment* 16(3):335-338.

The effect of elevated atmospheric CO₂ on water distribution in the intact roots of *Vicia faba* L. bean seedlings grown in natural soil was studied noninvasively with proton (H-1) nuclear magnetic resonance (NMR) imaging. Exposure of 24-d-old plants to atmospheric CO₂-enriched air at 650 μmol mol⁻¹ produced significant increases in water imaged in upper roots, hypogeal cotyledons and lower stems in response to a short-term drying-stress cycle. Above ground, drying produced negligible stem shrinkage and stomatal resistance was unchanged. In contrast, the same drying cycle caused significant depletion of water imaged in the same upper root structures in control plants subject to ambient CO₂ (350 μmol mol⁻¹), and stem shrinkage and increased stomatal resistance. The results suggest that inhibition of transpiration caused by elevated CO₂ does not necessarily result in attenuation of water transport from lower root structures. Inhibition of water loss from upper roots and lower stem in elevated CO₂ environments may be a mitigating factor in assessing deleterious effects of greenhouse changes on crops during periods of dry climate.

KEYWORDS: CARBONDIOXIDE, INSITU, MAGNETIC-RESONANCE MICROSCOPY, TRANSPORT

251

Bouma, T.J., K.L. Nielsen, D.M. Eissenstat, and J.P. Lynch. 1997. Estimating respiration of roots in soil: Interactions with soil CO₂, soil temperature and soil water content. *Plant and Soil* 195(2):221-232.

Little information is available on the variability of the dynamics of the actual and observed root respiration rate in relation to abiotic factors. In this study, we describe I) interactions between soil CO₂ concentration, temperature, soil water content and root respiration, and II) the effect of short-term fluctuations of these three environmental factors on the relation between actual and observed root respiration rates. We designed an automated, open gas-exchange system that allows continuous measurements on 12 chambers with intact roots in soil. By using three distinct chamber designs with each a different path for the air flow, we were able to measure root respiration over a 50-fold range of soil CO₂ concentrations (400 to 25000 ppm) and to separate the effect of irrigation on observed vs. actual root respiration rate. All respiration measurements were made on one-year-old citrus seedlings in sterilized sandy soil with minimal organic material. Root respiration was strongly affected by diurnal fluctuations in temperature (Q₁₀ = 2), which agrees well with the literature. In contrast to earlier findings for Douglas-fir (Qi et al., 1994), root respiration rates of citrus were not affected by soil CO₂ concentrations (400 to 25000 ppm CO₂; pH around 6). Soil CO₂ was strongly affected by soil water content but not by respiration measurements, unless the air flow for root respiration measurements was directed through the soil. The latter method of measuring root respiration reduced soil CO₂ concentration to that of incoming air. Irrigation caused a temporary reduction in CO₂ diffusion, decreasing the observed respiration rates obtained by techniques that depended on diffusion. This

apparent drop in respiration rate did not occur if the air flow was directed through the soil. Our dynamic data are used to indicate the optimal method of measuring root respiration in soil, in relation to the objectives and limitations of the experimental conditions.

KEYWORDS: CARBON DIOXIDE, DARK RESPIRATION, ELEVATED CO₂, ENRICHMENT, FIELD, GROWTH, PLANTS, RESPONSES, SEEDLINGS, SOUR ORANGE TREES

252

Bowden, R.D., K.M. Newkirk, and G.M. Rullo. 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. *Soil Biology and Biochemistry* 30(12):1591-1597.

Carbon dioxide and methane are important greenhouse gases whose exchange rates between soils and the atmosphere are controlled strongly by soil temperature and moisture. We made a laboratory investigation to quantify the relative importance of soil moisture and temperature on fluxes of CO₂ and CH₄ between forest soils and the atmosphere. Forest floor and mineral soil material were collected from a mixed hardwood forest at the Harvard Forest. Long-Term Ecological Research Site (MA) and were incubated in the laboratory under a range of moisture (air-dry to nearly saturated) and temperature conditions (5-25 degrees C). Carbon dioxide emissions increased exponentially with increasing temperature in forest floor material, with emissions reduced at the lowest and highest soil moisture contents. The forest floor Q(10) of 2.03 (from 15-25 degrees C) suggests that CO₂ emissions were controlled primarily by soil biological activity. Forest floor CO₂ emissions were predicted with a multiple polynomial regression model ($r^2 = 0.88$) of temperature and moisture, but the fit predicting mineral soil respiration was weaker ($r^2 = 0.59$). Methane uptake was controlled strongly by soil moisture, with reduced fluxes under conditions of very low or very high soil moisture contents. A multiple polynomial model accurately described CH₄ uptake by mineral soil material ($r^2 = 0.81$), but only weakly ($r^2 = 0.45$) predicted uptake by forest floor material. The mineral soil Q(10) of 1.11 for CH₄ uptake indicates that methane uptake is controlled primarily by physical processes. Our work suggests that inclusion of both moisture and temperature can improve predictions of soil CO₂ and CH₄ exchanges between soils and the atmosphere. Additionally, global change models need to consider interactions of temperature and moisture in evaluating effects of global climate change on trace gas fluxes. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC METHANE, CONSUMPTION, DYNAMICS, ECOSYSTEMS, NITROGEN, OXIDATION, RESPIRATION, RESPONSES, WATER

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Bowes, G. 1991. Growth at elevated CO₂ - photosynthetic responses mediated through rubisco. *Plant, Cell and Environment* 14(8):795-806.

The global uptake of CO₂ in photosynthesis is about 120 gigatons (Gt) of carbon per year. Virtually all passes through one enzyme, ribulose biphosphate carboxylase/oxygenase (rubisco), which initiates both the photosynthetic carbon reduction, and photorespiratory carbon oxidation, cycles. Both CO₂ and O₂ are substrates; CO₂ also activates the enzyme. In C₃ plants, rubisco has a low catalytic activity, operates below its K_m (CO₂), and is inhibited by O₂. Consequently, increases in the CO₂/O₂ ratio stimulate C₃ photosynthesis and inhibit photorespiration. CO₂ enrichment usually enhances the productivity of C₃ plants, but the effect is marginal in C₄ species. It also causes acclimation in various ways: anatomically, morphologically, physiologically or biochemically. So, CO₂ exerts secondary effects in growth regulation, probably at the molecular level, that are not predictable from its primary biochemical role in carboxylation. After an initial increase with CO₂ enrichment, net

photosynthesis often declines. This is a common acclimation phenomenon, less so in field studies, that is ultimately mediated by a decline in rubisco activity, though the RuBP/P(i)-regeneration capacities of the plant may play a role. The decline is due to decreased rubisco protein, activation state, and/or specific activity, and it maintains the rubisco fixation and RuBP/P(i)-regeneration capacities in balance. Carbohydrate accumulation is sometimes associated with reduced net photosynthesis, possibly causing feedback inhibition of the RuBP/P(i)-regeneration capacities, or chloroplast disruption. As exemplified by field-grown soybeans and salt marsh species, a reduction in net photosynthesis and rubisco activity is not inevitable under CO₂ enrichment. Strong sinks or rapid translocation may avoid such acclimation responses. Over geological time, aquatic autotrophs and terrestrial C₄ and CAM plants have genetically adapted to a decline in the external CO₂/O₂ ratio, by the development of mechanisms to concentrate CO₂ internally; thus circumventing O₂ inhibition of rubisco. Here rubisco affinity for CO₂ is less, but its catalytic activity is greater, a situation compatible with a high-CO₂ internal environment. In aquatic autotrophs, the CO₂ concentrating mechanisms acclimate to the external CO₂, being suppressed at high-CO₂. It is unclear, whether a doubling in atmospheric CO₂ will be sufficient to cause a de-adaptive trend in the rubisco kinetics of future C₃ plants, producing higher catalytic activities.

KEYWORDS: 1,5-DIPHOSPHATE CARBOXYLASE, CARBON-DIOXIDE CONCENTRATIONS, CO₂-ENRICHED ATMOSPHERE, ECHINOCHLOA CRUS GALLI, HIGH ATMOSPHERIC CO₂, KINETIC-PROPERTIES, LONG-TERM EXPOSURE, MONOECIOUS CUCUMBERS, PHOSPHOENOLPYRUVATE CARBOXYLASE, RIBULOSE BISPHOSPHATE CARBOXYLASE

254

Bowes, G. 1993. Facing the inevitable - plants and increasing atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology* 44:309-332.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CO₂-ENRICHMENT, ELEVATED CO₂, INORGANIC CARBON, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SHORT- TERM, SOURCE-SINK RELATIONS, SOYBEAN LEAVES

255

Bowes, G., J.C.V. Vu, M.W. Hussain, A.H. Pennanen, and L.H. Allen. 1996. An overview of how rubisco and carbohydrate metabolism may be regulated at elevated atmospheric [CO₂] and temperature. *Agricultural and Food Science in Finland* 5(3):261-270.

Although atmospheric CO₂ concentration ([CO₂]) has been up to 16-fold higher than at present, the past several million years have seen atypically low values. Thus, modern-day plants are adapted to cope with a low [CO₂]/[O₂] ratio. The present [CO₂] does not saturate C-3 photosynthesis, so its doubling produces an "efficiency effect", but it is not always fully realized. Acclimation to high [CO₂] during growth can down-regulate photosynthesis, presumably to optimize carbon acquisition and utilization. A primary factor in acclimation is a reduction in rubisco. Two crops, rice and soybean, were used to study this phenomenon. Rice photosynthesis and growth peaked at 500 μmol mol⁻¹, whereas soybean responded up to 990 μmol mol⁻¹. Rubisco concentration declined under CO₂-enrichment and increasing temperatures, more so in rice than soybean. The rubisco k_{cat} of rice was unaffected by growth [CO₂] or temperature, but that from soybean was increased by both. In rice the capacity to handle carbohydrate, as measured by sucrose phosphate synthase activity was up-regulated by CO₂-enrichment, but not by temperature. Leaf carbohydrates were increased by [CO₂], but decreased by higher temperatures, starch more

so than sucrose. Even though C-3 species differ in response to [CO₂] and temperature, CO₂-enrichment can moderate adverse effects of temperature extremes.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, CARBOXYLASE, EXPRESSION, GROWTH, LEAVES, PHOTOSYNTHESIS, PLANT-RESPONSES, RICE, SOURCE-SINK RELATIONS

256

Bowler, J.M., and M.C. Press. 1993. Growth-responses of 2 contrasting upland grass species to elevated CO₂ and nitrogen concentration. *New Phytologist* 124(3):515-522.

Growth parameters of *Agrostis capillaris* L. and *Nardus stricta* L. were measured in relation to ambient and elevated concentrations of CO₂ (340 and 550 μmol CO₂ l⁻¹, respectively) and at low and high concentrations of nitrogen (0.8 and 3 mmol NH₄NO₃, respectively). After 60 d of growth *A. capillaris* had attained approx. four times the total dry weight of *N. stricta* in all treatments, which was attributed to the greater leaf area ratio of the former. *A. capillaris* grown at the low nitrogen concentration attained 30% of the total dry weight of plants grown at high nitrogen. Over the 60 d period, destructive harvests (seven in total) showed the growth of *N. stricta* to be less sensitive than that of *A. capillaris* to the concentration of nitrogen, but in both species growth analysis showed the lower total dry weight at low nitrogen to be attributable to lower unit leaf rate. There was a differential response of both species to elevated concentrations of CO₂ which was nitrogen dependent. *A. capillaris* grown at elevated CO₂ attained a greater total dry weight than at ambient CO₂ and this response was proportionately greater at low nitrogen (78% increase) than at high nitrogen (58% increase). In contrast, in *N. stricta* there was no effect of CO₂ concentration on the total dry weight at low nitrogen whilst at high nitrogen plants grown at elevated CO₂ had a greater total dry weight after 48 d of growth. Calculation of the allometric coefficient (K) relating root growth to shoot growth indicated that the effect of the lower nitrogen concentration was to increase partitioning to the roots while the higher CO₂ concentration did not alter partitioning.

KEYWORDS: AVAILABILITY, CARBON-DIOXIDE ENRICHMENT, IRRADIANCE, MINERAL NUTRITION, PHOTOSYNTHESIS, PLANTS, SEEDLINGS, SOURCE-SINK RELATIONS, TEMPERATURE, WHEAT

257

Bowler, J.M., and M.C. Press. 1996. Effects of elevated CO₂, nitrogen form and concentration on growth and photosynthesis of a fast- and slow-growing grass. *New Phytologist* 132(3):391-401.

Growth and photosynthesis of *Agrostis capillaris* L. and *Nardus stricta* L. were measured for plants grown under ambient and elevated concentrations of CO₂ (340 and 550 μmol CO₂ l⁻¹) respectively) and a range of nitrogen concentrations (0.01, 0.1, 1 and 5 mg N l⁻¹) supplied as either ammonium sulphate or sodium nitrate. After 42 d of growth for *A. capillaris* and 49 d of growth for *N. stricta*, the higher nitrogen concentrations resulted in stimulation of growth. The form of nitrogen did not affect the total dry weight attained by *A. capillaris*. However, ammonium-grown *N. stricta* attained a greater total dry weight than did nitrate-grown plants. Nitrogen form influenced leaf area ratio, which was greater in nitrate-grown *A. capillaris* and in ammonium-grown *N. stricta*. At the two lowest nitrogen concentrations there was no effect of elevated CO₂ on total dry weight in either species, whilst at the two highest nitrogen concentrations positive growth responses to elevated CO₂ were observed. Photosynthetic capacity and carboxylation efficiency were lower in plants grown in elevated CO₂ at the two lowest nitrogen concentrations, and were associated with greater leaf soluble carbohydrate content and lower foliar nitrogen concentrations. By

contrast, the CO₂ treatment did not affect these parameters at the two highest nitrogen concentrations employed.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, EXPOSURE, GAS-EXCHANGE, HIGH ATMOSPHERIC CO₂, LEAVES, NUTRITION, PLANTS, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

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Brailsford, R.W., L.A.C.J. Voesenek, C.W.P.M. Blom, A.R. Smith, M.A. Hall, and M.B. Jackson. 1993. Enhanced ethylene production by primary roots of zea-mays L in response to sub-ambient partial pressures of oxygen. *Plant, Cell and Environment* 16(9):1071-1080.

Ethylene production by primary roots of 72-h-old intact seedlings of *Zea mays* L. cv. LG11 was studied under ambient and sub-ambient oxygen partial pressures (pO₂) using a gas flow-through system linked to a photoacoustic laser detector. Despite precautions to minimize physical perturbation to seedlings while setting-up, ethylene production in air was faster during the first 6h than later, in association with a small temporary swelling of the roots. When roots were switched from air (20.8kPa O₂) to 3 or 5kPa O₂ after 6h, ethylene production increased within 2-3h. When, the roots were returned to air 16h later, ethylene production decreased within 2-3h. The presence of 10kPa CO₂ did not interfere with the effect of 3kPa O₂. Transferring roots from air to 12.5kPa did not change ethylene production, while a reduction to 1kPa O₂ induced a small increase. The extra ethylene formed in 3 and 5kPa O₂ was associated with plagiotropism, swelling, root hair production, and after 72h, increased amounts of intercellular space (aerenchyma) in the root cortex. Root extension was also slowed down, but the pattern of response to oxygen shortage did not always match that of ethylene production. On return to air, subsequent growth patterns became normal within a few hours. In the complete absence of oxygen, no ethylene production was detected, even when anaerobic roots were returned to air after 16h.

KEYWORDS: ANOXIA, BIOSYNTHESIS, DEEP-WATER RICE, FORMING ENZYME, GROWTH, PLANTS, STIMULATION, SUBMERGENCE

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Brakke, M., and L.H. Allen. 1995. Gas-exchange of citrus seedlings at different temperatures, vapor-pressure deficits, and soil-water contents. *Journal of the American Society for Horticultural Science* 120(3):497-504.

Midday reductions of stomatal conductance and carbon dioxide assimilation rates (A(CO₂)) in Citrus are typically attributed to large leaf-to-air vapor-pressure differences or high atmospheric vapor-pressure deficits (VPD). This study investigated air temperature (T-a) and available soil water (ASW) level as corollary factors of atmospheric VPD that influence midday reduction of net gas exchange in citrus leaves. The influence of elevated atmospheric CO₂ under conditions that inhibit net canopy A(CO₂) was also investigated. Net canopy A(CO₂) and evapotranspiration rates of Carrizo citrange [Poncirus trifoliata Raf x Citrus sinensis (L.) Osbeck] and Swingle citrumelo (P. trifoliata Raf x C. paradisi Macf.) seedlings grown in outdoor controlled-environment growth chambers were measured under two levels of T-a with concomitant changes in VPD and two levels of atmospheric CO₂ concentration, which were changed in steps over time. Cyclical depletion of ASW was allowed to occur at each set of T-a/VPD and CO₂ combinations. Highest net canopy A(CO₂) rates at ambient CO₂ concentration (330 μmol . mol⁻¹) were obtained at the low T-a/VPD level (29C/2.4 kPa) and ASW >50%. Diurnal canopy CO₂ uptake rates decreased at the high T-a/VPD level (37C/3.6 kPa), and midday depression of canopy A(CO₂) was observed at ASW levels <50%. Net canopy A(CO₂) decreased at higher levels of ASW under the high T-

a/VPD treatment than at the low T-a/VPD treatment. At the elevated CO₂ concentration (840 μmol . mol⁻¹) net canopy CO₂ uptake rates were double those that occurred at ambient CO₂ levels and they did not exhibit midday reduction. Our data indicate that, when soil water is not readily available, citrus seedlings are more sensitive to high levels of T-a and VPD which results in reduction of CO₂ uptake. The inhibitory effects of elevated VPD and reduced ASW on citrus net A(CO₂) were lessened at the elevated atmospheric CO₂ level.

KEYWORDS: CARBON DIOXIDE, GROWTH, HUMIDITY, LEAVES, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION, TREES, VALENCIA ORANGE

260

Brandrud, T.E., and J.G.M. Roelofs. 1995. Enhanced growth of the macrophyte *Juncus bulbosus* in S Norwegian limed lakes. A regional survey. *Water, Air, and Soil Pollution* 85(2):913-918.

The effects of liming on the aquatic macrophyte vegetation have been investigated in S and SW Norway. In the western part of the study area, *Juncus bulbosus* was considerably more frequent in the limed than in the unlimed lakes, whilst in the eastern part there were no such differences, and the *J. bulbosus* populations were generally not so vital. In some southwestern areas a luxuriant and massive nuisance growth of *Juncus bulbosus* in the depth zone 0-4 m was recorded. The most vital plants produced up to 1 m long annual shoots, and developed extensive, dense and vital surface mats in shallow areas (depth zone 0-3 m) after 4-5 years. The original isoetid vegetation had disappeared in the areas of dense *J. bulbosus* populations, and this development seems to be more or less irreversible. The massive *J. bulbosus* expansion is seen mainly in directly limed lakes with a sometimes visible layer of calcium carbonate on the sediment surface, but enhanced growth has been observed also in lakes downstream liming. The massive expansion is believed to be due to an increase of CO₂ and ammonium in the sediment pore water, combined with a mild climate with a very high precipitation. In many areas the liming has led to an increase in species diversity, and a (re-)establishment of some acid-intolerant species such as *Myriophyllum alterniflorum* and *Potamogeton* spp.

KEYWORDS: ACIDIFICATION

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Bransby, D.I., S.B. McLaughlin, and D.J. Parrish. 1998. A review of carbon and nitrogen balances in switchgrass grown for energy. *Biomass & Bioenergy* 14(4):379-384.

Increased atmospheric CO₂, caused partly by burning fossil fuels, is assumed to elevate the risk of global warming, while nitrate contamination of surface runoff and groundwater from fertilizer and agricultural wastes constitutes a serious environmental hazard on a regional scale. Switchgrass (*Panicum virgatum* L.) grown as an energy crop could reduce atmospheric CO₂ accumulation by replacing fossil fuels and sequestering C. It could also improve soil productivity by C sequestration, and reduce NO₃-I contamination of water by absorbing N lost from fertilizer and agricultural waste if planted in filter strips on adjacent land. The objective of this study was to assess potential impacts of switchgrass on C and N balances by reviewing and synthesizing information from current literature, unpublished data and on-going research. Replacing fossil fuels with switchgrass, or any other biomass, will have a much greater effect on atmospheric CO₂ than C sequestration. This is because replacing fossil fuels provides a cumulative effect, while C sequestration offers only a one-time benefit. Furthermore, switchgrass will provide net gains in C sequestration only if it replaces annual row crops, but not if it replaces grazed pasture. Nitrogen recovery by switchgrass in an Alabama study was 65.6%, which compares favorably with the 50% recovery frequently quoted as

the norm for wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.). (C) 1998 Elsevier Science Ltd. All rights reserved.

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Brearley, J., M.A. Venis, and M.R. Blatt. 1997. The effect of elevated CO₂ concentrations on K⁺ and anion channels of *Vicia faba* L. guard cells. *Planta* 203(2):145-154.

The effects of elevated CO₂ concentrations on stomatal movement, anion- and K⁺-channel activities were examined in guard cells from epidermal strips of *Vicia faba*. Membrane voltage was measured using intracellular, double-barrelled microelectrodes and ion-channel currents were recorded under voltage clamp during exposure to media equilibrated with ambient (350 μmol l⁻¹), 1000 μmol l⁻¹ and 10 000 μmol l⁻¹ CO₂ in 20% O₂ and 80% N₂. The addition of 1000 μmol l⁻¹ CO₂ to the bathing solution caused stomata to close with a half-time of approx. 40 min, and with 10 000 μmol l⁻¹ CO₂ closure occurred with a similar time course. Under voltage clamp, exposure to 1000 μmol l⁻¹ and 10 000 μmol l⁻¹ CO₂ resulted in a rapid increase (mean, 1.5 ± 0.2-fold, n = 8; range 1.3- to 2.5-fold) in the magnitude of current carried by outward-rectifying K⁺ channels (I-K_{out}). The effect of CO₂ on I-K_{out} was essentially complete within 30 s and was independent of clamp voltage, but was associated with 25-40% (mean, 30 ± 4%) decrease in the half-time for current activation. Exposure to CO₂ also resulted in a four-fold increase in background current near the free-running membrane voltage, recorded as the instantaneous current at the start of depolarising and hyperpolarising voltage steps, and a decrease in the magnitude of current carried by inward-rectifying K⁺ channels (I-K_{in}). The effect of CO₂ on I-K_{in} was generally slower than on I-K_{out}; it was allied with a transient acceleration of its activation kinetics during the first 60-120 s of treatment; and it was associated with a negative shift in the voltage-sensitivity of gating over a period of 3-5 min. Measurements carried out to isolate the background currents attributable to anion channels (I-Cl_{in}), using tetraethylammonium chloride and CsCl, showed that CO₂ also stimulated I-Cl_{in} and dramatically altered its relaxation kinetics. Within the timeframe of CO₂ action at the membrane, no significant effect was observed on cytosolic pH, measured using the fluorescent dye 2',7'-bis-(2-carboxyethyl)-5,6-carboxyfluorescein (BCECF) and ratio fluorescence microphotometry. These results are broadly consistent with the pattern of guard-cell response to abscisic acid, and indicate that guard cells control both anion and K⁺ channels to achieve net solute loss in CO₂. By contrast with the effects of abscisic acid, however, the data indicate that CO₂ action is not mediated through changes in cytosolic pH and thereby implicate new and, as yet, unidentified pathway(s) for channel regulation in the guard cells.

KEYWORDS: ABSCISIC- ACID, CYTOSOLIC-FREE CALCIUM, ELECTRICAL CHARACTERISTICS, FUSICOCCIN ACTION, PLASMA-MEMBRANE, PROTEIN PHOSPHATASE, SIGNAL-TRANSDUCTION, STOMATAL CLOSURE, TRANSPORT, VOLTAGE

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Bremer, D.J., J.M. Ham, and C.E. Owensby. 1996. Effect of elevated atmospheric carbon dioxide and open-top chambers on transpiration in a tallgrass prairie. *Journal of Environmental Quality* 25(4):691-701.

Increasing concentrations of atmospheric carbon dioxide (CO₂) may influence plant-water relations in natural and agricultural ecosystems. A tallgrass prairie near Manhattan, KS, was exposed to elevated atmospheric CO₂ using open-top chambers (OTCs). Heat balance sap flow gauges were used to measure transpiration in ironweed [*Vernonia baldwini* var. *interior* (Small) Schub.], a C-3 forb, and on individual grass culms of big bluestem (*Andropogon gerardii* Vitman) and indiagrass [*Sorghastrum nutans* (L.) Nash], both C-4 grasses, in each

of three treatments: (i) CE (chamber enriched, 2x ambient CO₂); (ii) CA (chamber ambient, no CO₂ enrichment); and (iii) NC (no chamber, no CO₂ enrichment). Sap flow data were coupled with measurements of stomatal conductance, plant/canopy resistance, and whole-chamber evapotranspiration (ET) to determine the effect of elevated CO₂ on water use at different scales. Because of frequent rainfall during the study, all data were collected under well-watered conditions. Comparisons of CE and CA showed that sap flow was reduced by 33% in ironweed, 18% in big bluestem, and 22% in indiangrass under CO₂ enrichment. Whole-chamber ET was reduced by 23 to 27% under CO₂ enrichment. Comparisons of CA and NC showed that the environmental effect of the OTCs caused a 21 to 24% reduction in transpiration. Stomatal conductance decreased from 7.9 to 3.6 mm s⁻¹ in big bluestem and from 5.3 to 3.2 mm s⁻¹ in indiangrass under CO₂ enrichment. Soil water was consistently highest under elevated CO₂, reflecting the large reductions in transpiration. During sap flow measurements, whole-plant stomatal resistance to water vapor Bur in big bluestem increased from 103 to 194 s m⁻¹ under elevated CO₂.

KEYWORDS: CO₂, FLOW, PHOTOSYNTHESIS, RESPONSES, WATER RELATIONS

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Bremer, D.J., J.M. Ham, C.E. Owensby, and A.K. Knapp. 1998. Responses of soil respiration to clipping and grazing in a tallgrass prairie. *Journal of Environmental Quality* 27(6):1539-1548.

Soil-surface CO₂ flux (F-s) is an important component in prairie C budgets. Although grazing is common in grasslands, its effects on F-s have not been well documented. Three clipping treatments: (i) early-season clipping (EC); (ii) full-season clipping (FC); and (iii) no clipping (NC); which represented two grazing strategies and a control, were applied to plots in a tallgrass prairie in northeastern Kansas, USA. Measurements of F-s were made with a portable gas-exchange system at weekly to monthly intervals for 1 yr. Concurrent measurements of soil temperature and volumetric soil water content at 0.1 m were obtained with dual-probe heat-capacity sensors. Measurements of F-s also were obtained in grazed pastures. F-s ranged annually from 8.8 x 10⁻³ mg m⁻² s⁻¹ during the winter to 0.51 mg m⁻² s⁻¹ during the summer, following the patterns of soil temperature and canopy growth and phenology. Clipping typically reduced F-s 21 to 49% by the second day after clipping despite higher soil temperatures in clipped plots. Cumulative annual F-s were 4.94, 4.04, and 4.11 kg m⁻² yr⁻¹ in NC, EC, and FC treatments, respectively; thus, clipping reduced annual F-s by 17.5%. Differences in F-s between EC and FC were minimal, suggesting that different grazing strategies had little additional impact on annual F-s. Daily F-s in grazed pastures was 20 to 37% less than F-s in ungrazed pastures. Results suggest that grazing moderates F-s during the growing season by reducing canopy photosynthesis and slowing translocation of carbon to the rhizosphere.

KEYWORDS: ANDROPOGON-GERARDII, ATMOSPHERIC CO₂, CARBON, ELEVATED CO₂, EXCHANGE, FLUXES, PANICUM-VIRGATUM, PLANT, ROOT RESPIRATION, TEMPERATE GRASSLAND

265

Briones, G.L., P. Varoquaux, Y. Chambroy, J. Bouquant, G. Bureau, and B. Pascat. 1992. Storage of common mushroom under controlled atmospheres. *International Journal of Food Science and Technology* 27(5):493-505.

The effect of controlled atmosphere (CA) on the shelf-life of the common mushroom (*Agaricus bisporus*) was assessed using six parameters correlated with its commercial qualities. Low CO₂ concentrations (up to 2.5%) reduced brown discoloration compared to

the control in air. Higher CO₂ concentrations enhanced both internal and external browning. Low O₂ concentrations reduced growth of microorganisms, including pseudomonads. Respiration rate, when the mushrooms are placed again in normal air, is proportional to CO₂ concentration during storage suggesting that CO₂ exhibits a phytotoxic effect on mushrooms. A lower mannitol content was noted in mushrooms stored under CA than those stored in air (control). Mushrooms stored in a 5% CO₂ atmosphere for 7 days did not break their veil but their texture was very soft and spongy. Texture losses decreased when CO₂ concentrations increased.

KEYWORDS: AGARICUS-BISPORUS

266

Brioua, A.H., and C.T. Wheeler. 1994. Growth and nitrogen-fixation in *alnus-glutinosa* (L.) Gaertn under carbon-dioxide enrichment of the root atmosphere. *Plant and Soil* 162(2):183-191.

The effects of aeration of the N-free rooting medium with elevated CO₂ on (a) acetylene reduction by perlite-grown plants and (b) N₂-fixation and long-term growth of nutrient solution-grown plants were determined for nodulated *Alnus glutinosa* (L.) Gaertn. In the former experiments, roots of intact plants were incubated in acetylene in air in darkened glass jars for 3 hr, followed by a further 3 hr incubation period in air enriched with CO₂ (0-5%). During incubation, the CO₂ content of the jars increased by 0.17% per hour due to respiration of the root system, so that the CO₂ content at 3 hr was 0.5%. Additional enrichment of the rooting medium gas-phase with CO₂ equivalent to 1.1% and 1.75% CO₂ of the gas volume significantly increased nitrogenase activity (ethylene production) by 55% and 50% respectively, while enrichment with greater than 2.5% CO₂ decreased activity. In contrast, ethylene production by control plants, where CO₂ was not added to the assay jars, decreased by 8% over the assay period. In long-term growth experiments, nodulated roots of intact *Alnus glutinosa* plants were sealed into jars containing N-free nutrient solution (pH 6.3) and aerated with air, or air containing elevated levels of CO₂ (1.5% and 5%). Comparison of the appearance of CO₂-treated with air treated plants suggested that 1.5% CO₂ stimulated plant growth. However, at harvest after 5 or 6 weeks variability between plants masked the significance of differences in plant dry weight. A significant increase of 33% in total nitrogen of plants aerated with 1.5% CO₂, compared with air-treated plants, was demonstrated, broadly in line with the short-term increase in acetylene reducing activity observed following incubations with similar CO₂ concentrations. Shoot dry weight was not affected significantly by long-term exposure to 5% CO₂, the main effect on growth being a 20% reduction in dry weight of the root system, possibly through inhibition of root system respiration. However, in contrast to the inhibitory effects of high CO₂ on acetylene reduction there was no significant effect on the amounts of N₂ fixed.

KEYWORDS: ACETYLENE-REDUCTION, CO₂-ENRICHMENT, METABOLISM, N₂ FIXATION, NODULATION, NODULE DEVELOPMENT, PHOSPHOENOLPYRUVATE CARBOXYLASE, PHYSIOLOGY, PISUM-SATIVUM, RESPIRATION

267

Britz, S.J., D.T. Krizek, D.R. Lee, W.G. Harris, W.E. Hungerford, and W.A. Bailey. 1993. Soybean growth under microwave-powered lamps, high-irradiance-discharge lamps, or solar-radiation at ambient or elevated CO₂. *Plant Physiology* 102(1):141.

268

Brklacich, M., P. Curran, and D. Brunt. 1996. The application of agricultural land rating and crop models to CO₂ and climate change

issues in Northern regions: The Mackenzie Basin case study. *Agricultural and Food Science in Finland* 5(3):351-365.

The Mackenzie Basin in northwestern Canada covers approximately 1.8 million km² and extends from 52 degrees N to 70 degrees N. Much of the Basin is currently too cool and remote from markets to support a viable agricultural sector, but the southern portion of the Basin has the physical potential to support commercial agriculture. This case study employed agricultural land rating and crop models to estimate the degree to which a CO₂-induced global warming might alter the physical potential for commercial agriculture throughout the Basin. The two climate change scenarios considered in this analysis would relax the current constraints imposed by a short and cool frost-free season, but without adaptive measures, drier conditions and accelerated crop development rates were estimated to offset potential gains stemming from elevated CO₂ levels and warmer temperatures. In addition to striving for a better understanding of the extent to which physical constraints on agriculture might be modified by climate change, there is a need to expand the research context and to consider the capacity of agriculture to adapt to altered climates.

KEYWORDS: CANADA

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Broadmeadow, M.S.J., J. Heath, and T.J. Randle. 1999. Environmental limitations to O₃ uptake - Some key results from young trees growing at elevated CO₂ concentrations. *Water, Air, and Soil Pollution* 116(1-2):299-310.

Elevated carbon dioxide concentrations and limited water supply have been shown to reduce the impact of ozone pollution on the growth and physiology of *Quercus petraea* in a long-term factorial experiment. These responses can be explained by observed reductions in stomatal conductance, and thus potential ozone exposure of 28% and 40% for CO₂ and drought treatments respectively. However, parameterisation of a stomatal conductance model for *Quercus robur* and *Fagus sylvatica* grown under ambient and elevated CO₂ concentrations in a separate experiment has demonstrated that elevated CO₂ also reduces the responsiveness of stomata to both saturation deficit (LAVPD) and soil moisture deficit (psi) in beech, and to a lesser extent, in oak. Season-long model simulations of ozone fluxes suggest that LAVPD and psi conductance parameters derived at ambient CO₂ concentrations will lead to these fluxes being underestimated by 24% and 2% for beech and oak respectively at 615 ppm CO₂.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, FOREST TREES, GAS-EXCHANGE, OZONE UPTAKE, PLANTS, SENSITIVITY, SITCHENSIS BONG CARR, STOMATAL RESPONSE

270

Brooks, G.L., and J.B. Whittaker. 1998. Responses of multiple generations of *Gastrophysa viridula*, feeding on *Rumex obtusifolius*, to elevated CO₂. *Global Change Biology* 4(1):63-75.

Rumex obtusifolius plants and three generations of the tri-voltine leaf beetle *Gastrophysa viridula* were simultaneously exposed to elevated CO₂ (600 ppm) to determine its effect on plant quality and insect performance. This exposure resulted in a reduction in leaf nitrogen, an increase in the C/N ratio and lower concentrations of oxalate in the leaves than in ambient air (350 ppm). Despite these changes in food quality, the effect of elevated CO₂ on larvae of *Gastrophysa viridula* over three generations was minimal. However, the effect of CO₂ did differ slightly between the generations of the insect. For the first generation, the results obtained were different from many of the published results in that elevated CO₂ had no measurable effects on

performance, except that third instar larvae showed compensatory feeding. Food quality, including leaf nitrogen content, declined over time in material grown in both ambient and elevated CO₂. The results obtained for the second generation were similar to the first except that first instar larvae showed reduced relative growth rate in elevated CO₂. Development time from hatching to pupation decreased over each generation, probably as a result of increasing temperatures. Measurements of adult performance showed that fecundity at the end of the second generation was reduced relative to the first, in line with the reduction in food quality. In addition at the end of the second generation, but not at the end of the first generation, adult females in elevated CO₂ laid 30% fewer eggs per day and the eggs laid were 15% lighter than those in ambient conditions. These lighter eggs, coupled with no effect of elevated CO₂ on growth during the third generation, meant that the larvae were consistently smaller in elevated CO₂ during this generation. These results offer further insights into the effect that elevated CO₂ will have on insect herbivores and provide a more detailed basis for population predictions.

KEYWORDS: CARBON DIOXIDE, DIETARY NITROGEN, GAS-EXCHANGE, GROWTH, JUNONIA-COENIA, LARVAE, LEPIDOPTERA, MANDUCA-SEXTA CATERPILLARS, NUTRITIONAL ECOLOGY, PERFORMANCE

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Brooks, G.L., and J.B. Whittaker. 1999. Responses of three generations of a xylem-feeding insect, *Neophilaenus lineatus* (Homoptera), to elevated CO₂. *Global Change Biology* 5(4):395-401.

A population of the xylem-feeding spittlebug, *Neophilaenus lineatus*, on blocks of natural vegetation transferred to large hemispherical chambers was studied over two generations with continuous exposure to elevated CO₂ (600 ppm). The third generation was transferred from the blocks to potted *Juncus squarrosus* to enable measurements of fecundity. The principal food plant throughout was *Juncus squarrosus*. Survival of the nymphs was reduced by more than 20% in elevated CO₂ relative to ambient (350 ppm) in both years of the main experiment. Elevated CO₂ also delayed development by one or more nymphal instars in each year. Fecundity was not significantly affected. The C/N ratio of whole *Juncus* leaves was increased in elevated CO₂ and the transpiration rates of the plants were reduced. These changes may have been responsible for the effect of elevated CO₂ on spittlebug performance. However, other factors such as plant architecture and microclimate may also be important.

KEYWORDS: CICADELLIDAE, FLUID, GROWTH, HOMALODISCA-COAGULATA, LEAFHOPPER, PERFORMANCE, PREFERENCE, RUMEX, SAP, SPITTLEBUG

272

Brooks, J.R., L.B. Flanagan, N. Buchmann, and J.R. Ehleringer. 1997. Carbon isotope composition of boreal plants: Functional grouping of life forms. *Oecologia* 110(3):301-311.

We tested the hypothesis that life forms (trees, shrubs, forbs, and mosses; deciduous or evergreen) can be used to group plants with similar physiological characteristics. Carbon isotope ratios ($\delta^{13}\text{C}$) and carbon isotope discrimination (Δ) were used as functional characteristics because $\delta^{13}\text{C}$ and Δ integrate information about CO₂ and water fluxes, and so are useful in global change and scaling studies. We examined $\delta^{13}\text{C}$ values of the dominant species in three boreal forest ecosystems: wet *Picea mariana* stands, mesic *Populus tremuloides* stands, and dry *Pinus banksiana* stands. Life form groups explained a significant fraction of the variation in leaf carbon isotope composition; seven life-form categories explained 50% of the variation in $\delta^{13}\text{C}$ and 42% of the variation in Δ and 52% of the variance

not due to intraspecific genetic differences (n=335). The life forms were ranked in the following order based on their values: evergreen trees < deciduous trees = evergreen and deciduous shrubs = evergreen forbs < deciduous forbs = mosses. This ranking of the life forms differed between deciduous (*Populus*) and evergreen (*Pinus* and *Picea*) ecosystems. Furthermore, life forms in the *Populus* ecosystem had higher discrimination values than life forms in the dry *Pinus* ecosystem; the *Picea* ecosystem had intermediate Delta values. These correlations between Delta and life form were related to differences in plant stature and leaf longevity. Shorter plants had lower Delta values than taller plants, resulting from reduced light intensity at lower levels in the forest. After height differences were accounted for, deciduous leaves had higher discrimination values than evergreen leaves, indicating that deciduous leaves maintained higher ratios of intracellular to ambient CO₂ (c(i)/c(a)) than did evergreen leaves in a similar environment within these boreal ecosystems. We found the same pattern of carbon isotope discrimination in a year with above-average precipitation as in a year with below-average precipitation, indicating that environmental fluctuations did not affect the ranking of life forms. Furthermore, plants from sites near the northern and southern boundaries of the boreal forest had similar patterns of discrimination. We concluded that life forms are robust indicators of functional groups that are related to carbon and water fluxes within boreal ecosystems.

KEYWORDS: C-13, COMMUNITIES, CONSEQUENCES, DISCRIMINATION, FOREST, MODEL, PHOTOSYNTHESIS, TEMPERATURE, TRANSPIRATION, WATER-USE EFFICIENCY

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Brooks, J.R., L.B. Flanagan, G.T. Varney, and J.R. Ehleringer. 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO₂ within boreal forest canopies. *Tree Physiology* 17(1):1-12.

We compared vertical gradients in leaf gas exchange, CO₂ concentrations, and refixation of respired CO₂ in stands of *Populus tremuloides* Michx., *Pinus banksiana* Lamb. and *Picea mariana* (Mill.) B.S.P. at the northern and southern boundaries of the central Canadian boreal forest. Midsummer gas exchange rates in *Populus tremuloides* were over twice those of the two conifer species, and *Pinus banksiana* rates were greater than *Picea mariana* rates. Gas exchange differences among the species were attributed to variation in leaf nitrogen concentration. Despite these differences, ratios of intercellular CO₂ to ambient CO₂ (c(i)/c(a)) were similar among species, indicating a common balance between photosynthesis and stomatal conductance in boreal trees. At night, CO₂ concentrations were high and vertically stratified within the canopy, with maximum concentrations near the soil surface. Daytime CO₂ gradients were reduced and concentrations throughout the canopy were similar to the CO₂ concentration in the well-mixed atmosphere above the canopy space. Photosynthesis had a diurnal pattern opposite to the CO₂ profile, with the highest rates of photosynthesis occurring when CO₂ concentrations and gradients were lowest. After accounting for this diurnal interaction, we determined that photosynthesizing leaves in the understory experienced greater daily CO₂ concentrations than leaves at the top of the canopy. These elevated CO₂ concentrations were the result of plant and soil respiration. We estimated that understory leaves in the *Picea mariana* and *Pinus banksiana* stands gained approximately 5 to 6% of their carbon from respired CO₂.

KEYWORDS: ATMOSPHERE, CARBON ISOTOPE DISCRIMINATION, DIOXIDE, PLANTS, RATIOS, SEEDLINGS, SPATIAL VARIATION, STOMATAL CONDUCTANCE, TEMPERATURE, USE EFFICIENCY

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Brooks, P.D., D.H. Campbell, K.A. Tonnessen, and K. Heuer. 1999.

Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. *Hydrological Processes* 13(14-15):2191-2201.

The causes of natural variability in catchment scale N export need to be understood and quantified before the effects of increased N deposition in high elevation catchments can be evaluated. This study evaluates controls on the size of the leachable soil N pool concurrent with the spring hydrologic flush that is primarily responsible for the transport of N to surface water. In high elevation catchments in the western United States, sources of N during this snowmelt flush include both atmospheric N deposition stored in the snowpack until melt and mobile soil N pools, and sinks are dominated by biogeochemical processes that occur in soil under snow cover. Because soil processes may serve either as a source or sink for N, controls on the amount of inorganic N leached from soil during the snowmelt period were evaluated in the major landscape types in four catchments in Colorado. Measurements of leached N were inversely related to measurements of over-winter CO₂ flux at all sites, indicating that N was immobilized in soil heterotrophic biomass. Because over-winter soil heterotrophic activity is controlled primarily by the depth and timing of snow accumulation, the importance of these plot scale measurements to catchment scale N export were evaluated using a long-term record of winter precipitation, N deposition, and N export from Loch Vale in Rocky Mountain National Park. This data set identified a strong, linear relationship (r(2) = 0.68) between catchment scale N retention and winter snow cover, consistent with subnivean, soil based controls on the mobile N pool identified at the plot scale. These results indicate that the winter snow pack is the major control both on hydrologic N export and on soil source/sink relationships for N concurrent with this transport mechanism. The effect of winter snow cover on the fate of both atmospheric and soil N needs to be considered when evaluating potential the effects of increased N deposition on either terrestrial or aquatic ecosystems in seasonally snow-covered watersheds. In these systems, changes in surface water chemistry are likely to occur in high deposition, snow-covered sites during low snow years before terrestrial vegetation is affected. Copyright (C) 1999 John Wiley & Sons, Ltd.

KEYWORDS: ALPINE TUNDRA, CO₂, COLORADO, FLUX, FOREST, FRONT RANGE, INORGANIC NITROGEN, NITROGEN MINERALIZATION, NIWOT RIDGE, SATURATION

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Brown, K.R. 1991. Carbon-dioxide enrichment accelerates the decline in nutrient status and relative growth-rate of *Populus tremuloides* Michx seedlings. *Tree Physiology* 8(2):161-173.

Changes in growth dynamics and mineral nutrient concentrations were measured in *Populus tremuloides* Michx., trembling aspen, grown for 100 days following germination in atmospheres containing 350 or 750- μ mol l⁻¹ CO₂. Seedlings were fertilized with nitrogen (N) at concentrations of 15.5 mM (high-N), 1.55 mM (medium-N), or 0.155 mM (low-N). Initially, relative growth rates were enhanced by CO₂ enrichment in each N regime, but the effects did not persist. In plants grown in high-N or medium-N, foliar concentrations of Ca and Mg decreased in response to CO₂ enrichment. During the 100-day study, whole-plant concentrations of N and P decreased in all treatments. The decreases in mineral nutrient concentrations over time were accelerated in CO₂-enriched plants and accompanied the disappearance of the CO₂-induced growth enhancement. It is concluded that the depression of relative growth rates often associated with long-term CO₂ enrichment of plants may result from decreases in plant nutrient status.

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Brown, R.A., and N.J. Rosenberg. 1999. Climate change impacts on

the potential productivity of corn and winter wheat in their primary United States growing regions. *Climatic Change* 41(1):73-107.

We calculate the impacts of climate effects inferred from three atmospheric general circulation models (GCMs) at three levels of climate change severity associated with change in global mean temperature (GMT) of 1.0, 2.5 and 5.0 degrees C and three levels of atmospheric CO₂ concentration ([CO₂]) - 365 (no CO₂ fertilization effect), 560 and 750 ppm - on the potential production of dryland winter wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) for the primary (current) U.S. growing regions of each crop. This analysis is a subset of the Global Change Assessment Model (GCAM) which has the goal of integrating the linkages and feedbacks among human activities and resulting greenhouse gas emissions, changes in atmospheric composition and resulting climate change, and impacts on terrestrial systems. A set of representative farms was designed for each of the primary production regions studied and the Erosion Productivity Impact Calculator (EPIC) was used to simulate crop response to climate change. The GCMs applied were the Goddard Institute of Space Studies (GISS), the United Kingdom Meteorological Transient (UKTR) and the Australian Bureau of Meteorological Research Center (BMRC), each regionalized by means of a scenario generator (SCENGEN). The GISS scenarios have the least impact on corn and wheat production, reducing national potential production for corn by 6% and wheat by 7% at a GMT of 2.5 degrees C and no CO₂ fertilization effect, the UKTR scenario had the most severe impact on wheat, reducing production by 18% under the same conditions; BMRC had the greatest negative impact on corn, reducing production by 20%. A GMT increase of 1.0 degrees marginally decreased corn and wheat production. Increasing GMT had a detrimental impact on both corn and wheat production, with wheat production suffering the greatest losses. Decreases for wheat production at GMT 5.0 and [CO₂] = 365 ppm range from 36% for the GISS to 76% for the UKTR scenario. Increases in atmospheric [CO₂] had a positive impact on both corn and wheat production. At GMT 1.0, an increase in [CO₂] to 560 ppm resulted in a net increase in corn and wheat production above baseline levels (from 18 to 29% for wheat and 2 to 5% for corn). Increases in [CO₂] help to offset yield reductions at higher GMT levels; in most cases, however, these increases are not sufficient to return crop production to baseline levels.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO₂, EPIC MODEL, EROSION, METHODOLOGY, RESPONSES, SENSITIVITY, SIMULATION, VARIABILITY, YIELD

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Brown, S., C.A.S. Hall, W. Knabe, J. Raich, M.C. Trexler, and P. Woerner. 1993. Tropical forests - their past, present, and potential future - role in the terrestrial carbon budget. *Water, Air, and Soil Pollution* 70(1-4):71-94.

In this paper we review results of research to summarize the state-of-knowledge of the past, present, and potential future roles of tropical forests in the global C cycle. In the pre-industrial period (ca. 1850), the flux from changes in tropical land use amounted to a small C source of about 0.06 Pg yr⁻¹. By 1990, the C source had increased to 1.7 +/- 0.5 Pg yr⁻¹. The C pools in forest vegetation and soils in 1990 was estimated to be 159 Pg and 216 Pg, respectively. No concrete evidence is available for predicting how tropical forest ecosystems are likely to respond to CO₂ enrichment and/or climate change. However, C sources from continuing deforestation are likely to overwhelm any change in C fluxes unless land management efforts become more aggressive. Future changes in land use under a "business as usual" scenario could release 41-77 Pg C over the next 60 yr. Carbon fluxes from losses in tropical forests may be lessened by aggressively pursued agricultural and forestry measures. These measures could reduce the magnitude of the tropical C source by 50 Pg by the year 2050. Policies to mitigate C losses must be multiple and concurrent, including reform of forestry, land tenure, arid

agricultural policies, forest protection, promotion of on-farm forestry, and establishment of plantations on non-forested lands. Policies should support improved agricultural productivity, especially replacing non-traditional slash-and-burn agriculture with more sustainable and approaches.

KEYWORDS: ATMOSPHERIC CO₂, BIOMASS, CYCLE, DIOXIDE, LAND-USE CHANGE, MODEL, NET, ORGANIC-MATTER, PRIMARY PRODUCTIVITY, SINKS

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Bryant, J., G. Taylor, and M. Frehner. 1998. Photosynthetic acclimation to elevated CO₂ is modified by source : sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment* 21(2):159-168.

Artificial chalk grassland swards were exposed to either ambient air or air enriched to 600 $\mu\text{mol mol}^{-1}$ CO₂, using free-air CO₂ enrichment technology, and subjected to an 8 week simulated grazing regime. After 14 months of treatment, ribulose-1,5-bisphosphate carboxylase (Rubisco) activity (V_c, V_{max}) and electron transport mediated ribulose-1,5-bisphosphate (RuBP) regeneration capacity (J_{max}), estimated from leaf gas exchange, were significantly lower in fully expanded leaves of *Anthyllis vulneraria* L. (a legume) and *Sanguisorba minor* Scop, grown in elevated CO₂. After a change in source:sink balance brought about by defoliation, photosynthetic capacity was fully restored in *A. vulneraria* and *S. minor*, but acclimation continued in the grass *Bromopsis erecta* (Hudson) Fourr. Changes in net photosynthesis (P_n) with growth at elevated CO₂ ranged from a 1.6% reduction in pre-cut leaves of *A. vulneraria* to a 47.1% stimulation in postcut leaves of *S. minor*. Stomatal acclimation was observed in leaves of *A. vulneraria* (reduced stomatal density) and *B. erecta* (reduced stomatal conductance). The results are discussed in terms of whole-plant resource-use optimization and chalk grassland community competitive interactions at elevated CO₂.

KEYWORDS: ATMOSPHERIC CO₂, BIOCHEMISTRY, C-3, GAS-EXCHANGE, LEAVES, METABOLISM, PLANT GROWTH, STOMATAL DENSITY

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Bucher, J.B., D.P. Tarjan, R.T.W. Siegwolf, M. Saurer, H. Blum, and G.R. Hendrey. 1998. Growth of a deciduous tree seedling community in response to elevated CO₂ and nutrient supply. *Chemosphere* 36(4-5):777-782.

In a FACE experiment, one year old alder, ash, beech, and oak seedlings were planted together in tubs containing calcareous sandy alluvial soil with or without a slow release NPK- fertilizer, and exposed to ambient and elevated CO₂ concentrations (360 and 600 $\mu\text{mol l}^{-1}$) for 20 weeks. In addition to the fertilizer, all tubs received N-15-ammonium nitrate as a marker. Elevated CO₂ significantly increased biomass production in alder, but had no effect on oak and ash. In beech, due to disease and mortality in all treatments, any possible effects were obscured. The addition of fertilizer had no effect on biomass production in alder, but increased production in oak and ash significantly. In oak a treatment synergism may be present. The non-appearance of a synergistic CO₂ and fertilizer effect in alder may be explained by a fertilizer induced reduction of the N-fixing root-nodule biomass concurrent with a switch of the N-assimilation from atmospheric N to soil N supply, as the $\delta^{15}\text{N}$ measurements in the leaves of alder as opposed to oak indicate. Although elevated CO₂ resulted in a significant biomass increase in alder, it did not lead to an appreciable increase in the proportional presence of the species as measured on total plant biomass in the tub. Increasing the nutrient supply in the soil, however,

did lead to appreciable gains in the proportional presence of oak and ash.

KEYWORDS: ATMOSPHERE, ECOSYSTEMS, ENRICHMENT

280

Buchi, R., M. Bachmann, and F. Keller. 1998. Carbohydrate metabolism in source leaves of sweet basil (*Ocimum basilicum* L.), a starch-storing and stachyose-translocating labiate. *Journal of Plant Physiology* 153(3-4):308-315.

Sweet basil (*Ocimum basilicum* L.) is an annual aromatic herb that grows in temperate to tropical regions. During ontogeny, the predominant non-structural carbohydrate of mature leaves of plants older than 2 months after sowing was starch (up to 66 mg.g fresh weight(-1)), followed by the raffinose family oligosaccharides (RFO) and galactinol (metabolic RFO precursor) (both up to 1.0 mg.g fresh weight(-1)). Sucrose was only a minor component (up to 0.5 mg.g fresh weight(-1)). All of these carbohydrates displayed distinct diurnal patterns with an increase during the day and a decrease during the night. Starch concentrations showed the most pronounced diurnal change, with an almost tenfold increase during the day. A treatment combining leaf excision, continuous illumination, and high CO₂ levels was aimed at elevating the leaf carbohydrate status and resulted in an increase of the concentrations of starch and soluble carbohydrates (mainly glucose and fructose) of 60- and 12-fold, respectively. We conclude that sweet basil leaves use starch as their main storage carbohydrate, and not RFO or sucrose. Phloem exudates were collected by the classical EDTA- method and analyzed by HPLC. More than 85 % of the translocated sugars were RFO (mainly stachyose) and only 5 % sucrose. To study the tissue compartmentation of stachyose synthesis in source leaves, leaf pieces and mesophyll protoplasts isolated from them were compared. Stachyose and its anabolic enzyme, stachyose synthase, were totally absent from mesophyll protoplasts. Likewise, isolated mesophyll protoplasts were not capable of photosynthesizing [C-14]stachyose from (CO₂)-C-14, even after GO min, whereas osmotically stressed leaf pieces were. These results are in support of the current polymer tray model of symplastic phloem loading of stachyose, which states that stachyose is synthesized in the intermediary cells of minor vein phloem.

KEYWORDS: ACCUMULATION, AJUGA- REPTANS L, CELL, COMPARTMENTATION, CUCUMIS-MELO L, DIURNAL PATTERN, MESOPHYLL, MINOR-VEIN ANATOMY, PROTOPLASTS, RAFFINOSE FAMILY OLIGOSACCHARIDES

281

Buchmann, N., J.R. Brooks, K.D. Rapp, and J.R. Ehleringer. 1996. Carbon isotope composition of C-4 grasses is influenced by light and water supply. *Plant, Cell and Environment* 19(4):392-402.

The carbon isotope composition of C-4 grasses has the potential to be used as an indicator of changes in the isotopic composition and concentration of atmospheric CO₂, especially for climate reconstruction. The usefulness of C-4 grasses for this purpose hinges on the assumption that their photosynthetic discrimination against C-13 remains constant in a wide range of environmental conditions. We tested this assumption by examining the effects of light and water stress on the carbon isotope composition of C-4 grasses using different biochemical subtypes (NADP-ME, NAD-ME, PCK) in glasshouse experiments. We grew 14 different C-4 grass species in four treatments: sun-watered, sun-drought, shade-watered and shade-drought. Carbon isotope discrimination (Delta) rarely remained constant. In general, Delta values were lowest in sun-watered grasses, greater for sun-drought plants and even higher for plants of the shade-watered treatment. The highest Delta values were generally found in the most stressed grasses, the shade-drought plants. Grasses of the NADP-ME subtype were the least influenced by a change in environmental variables, followed by PCK and NAD-ME subtypes.

Water availability affected the carbon isotope discrimination less than light limitation in PCK and NAD-ME subtypes, but similarly in NADP-ME subtypes. In another experiment, we studied the effect of increasing light levels (150 to 1500 mu mol photons m(-2) s(-1)) on the Delta values of 18 well-watered C-4 grass species. Carbon isotope discrimination remained constant until photon flux density (PFD) was less than 700 mu mol photons m(-2) s(-1). Below this light level, Delta values increased with decreasing irradiance for all biochemical subtypes. The change in Delta was less pronounced in NADP-ME and PCK than in NAD-ME grasses. Grasses grown in the field and in the glasshouse showed a similar pattern. Thus, caution should be exercised when using C-4 plants under varying environmental conditions to monitor the concentration or carbon isotopic composition of atmospheric CO₂ in field/glasshouse studies or climate reconstruction.

KEYWORDS: ATMOSPHERIC CO₂, C-4 PLANTS, CO₂ ASSIMILATION, DISCRIMINATION, IRRADIANCE, LEAF CONDUCTANCE, LEAVES, NUTRITION, PARTIAL-PRESSURE, PHOTOSYNTHESIS

282

Buddendorffjoosten, J.M.C., and E.J. Woltering. 1994. Components of the gaseous environment and their effects on plant-growth and development in-vitro. *Plant Growth Regulation* 15(1):1-16.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, CONTROLLED INVITRO ENVIRONMENT, DENOVO SHOOT REGENERATION, ETHYLENE INHIBITORS, PHOTOSYNTHETIC CHARACTERISTICS, STAGE-II MICROPROPAGATION, STRAWBERRY PLANTLETS, TISSUE-CULTURE, VOLATILE EMISSIONS

283

Bugbee, B., B. Spanarkel, S. Johnson, O. Monje, and G. Koerner. 1994. CO₂ crop growth enhancement and toxicity in wheat and rice. *Life Sciences and Space Research XXV (3) 14(11):257-267.*

The effects of elevated CO₂ on plant growth are reviewed and the implications for crop yields in regenerative systems are discussed. There is considerable theoretical and experimental evidence indicating that the beneficial effects of CO₂ are saturated at about 0.12% CO₂ in air. However, CO₂ can easily rise above 1% of the total gas in a closed system, and we have thus studied continuous exposure to CO₂ levels as high as 2%. Elevating CO₂ from 340 to 1200 mu mol mol(-1) can increase the seed yield of wheat and rice by 30 to 40%; unfortunately, further CO₂ elevation to 2500 mu mol mol(-1) (0.25%) has consistently reduced yield by 25% compared to plants grown at 1200 mu mol mol(-1); fortunately, there was only an additional 10% decrease in yield as the CO₂ level was further elevated to 2% (20,000 mu mol mol(-1)). Yield increases in both rice and wheat were primarily the result of increased number of heads per m², with minor effects on seed number per head and seed size. Yield increases were greatest in the highest photosynthetic photon flux. We used photosynthetic gas exchange to analyze CO₂ effects on radiation interception, canopy quantum yield, and canopy carbon use efficiency. We were surprised to find that radiation interception during early growth was not improved by elevated CO₂. As expected, CO₂ increased quantum yield, but there was also a small increase in carbon use efficiency. Super-optimal CO₂ levels did not reduce vegetative growth, but decreased seed set and thus yield. The reduced seed set is not visually apparent until final yield is measured. The physiological mechanism underlying CO₂ toxicity is not yet known, but elevated CO₂ levels (0.1 to 1% CO₂) increase ethylene synthesis in some plants and ethylene is a potent inhibitor of seed set in wheat.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-4 PLANTS, ELEVATED CO₂, ETHYLENE RELEASE, LONG-TERM

284

Bugmann, H. 1997. Sensitivity of forests in the European Alps to future climatic change. *Climate Research* 8(1):35-44.

Model-based assessments of the impacts of climatic change on forests are confronted with 2 fundamental problems: first, there is a considerable uncertainty in the predictions of future climate; second, the forest models contain simplified parameterizations of ecological processes. In this paper, the sensitivity of forest models to different steady-state climate scenarios, to different process formulations and to different assumptions on the transient behaviour of climate is studied. The effects of 3 scenarios of climatic change and the behaviour of 5 forest gap models of the FORECE/FORCLIM family are compared at sites along an elevational gradient in the European Alps. A wide variety of species compositions may be obtained at a given site depending on the scenario of future climate. At some sites all future forests differ radically from today's forest, suggesting that these current forests are highly sensitive to climatic change. At some sites, the results of the 5 forest models differ strongly with respect to species composition and carbon storage when subjected to the same climate scenario, showing that the models need to be improved in order to arrive at reliable and robust parameterizations of abiotic and biotic influences in forest models. When comparing the effects of step, Linear, and sigmoid changes of the mean climatic parameters over 100 yr, it becomes evident that the type of change modelled is not crucial because the climatic change proceeds fast compared to the successional dynamics. It is concluded that simulations of the possible effects of climatic change on forests should be considered as sensitivity tests, not as predictions. Given the current uncertainties in atmospheric sciences (climate predictions) and in ecology (modelling of long-term forest dynamics), the most promising research strategy is to compare the effects of several climate scenarios and the projections of several forest models to arrive at state-of-the-art ecological impact assessments.

KEYWORDS: CO₂, MATTER, MODEL

285

Bukhov, N.G., N. Boucher, and R. Carpentier. 1997. Aftereffect of short-term heat shock on photosynthetic reactions in barley leaves. *Russian Journal of Plant Physiology* 44(4):526-532.

Effects of preheating 8- to 10-day-old barley (*Hordeum vulgare* L.) leaves at 40-46 degrees C on oxygen evolution, chlorophyll fluorescence, and photoacoustic signals were examined. Preheating of leaves at 40 degrees C led to a threefold decrease in the initial slope of the light-response curve of photosynthesis and a marked enhancement of the nonphotochemical quenching of chlorophyll fluorescence, which indicates a drastic increase in the nonradiative dissipation of absorbed light quanta. The maximum photosynthetic activity attained at saturating light and elevated CO₂ concentration was suppressed by this heat treatment by no more than 30%. The photochemical activity of PS II reaction centers in dark-adapted leaves also decreased to the same extent after the heat treatment. In preheated leaves, strong light pulses increased the photobaric component of the photoacoustic signal (measured at 35 Hz) instead of suppressing the signal. The magnitude of the rise-phase of the photoacoustic signal increased with the preheating temperature. An enhancement of the photoacoustic signal induced by strong light pulses was also observed in leaves in which the normal photosynthetic process was disturbed by feeding them methylviologen. It is concluded that the short-term heating of leaves impairs photochemical conversion of light quanta in reaction centers of PS II due to an increase in the magnitude of the proton gradient across the thylakoid membrane. This indicates that dark reactions of photosynthesis in preheated leaves

cannot efficiently use the ATP and reduced NADP formed in the course of photosynthetic electron transport.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, CHLOROPLASTS, INDUCTION, OXYGEN EVOLUTION, PHOTOINHIBITION, PHOTOSYSTEM-I, RESOLUTION, SPINACH LEAVES, STIMULATION, TEMPERATURE

286

Bunce, J.A. 1992. Light, temperature and nutrients as factors in photosynthetic adjustment to an elevated concentration of carbon-dioxide. *Physiologia Plantarum* 86(1):173-179.

The short-term stimulation of the net rate of carbon dioxide exchange of leaves by elevated concentrations of CO₂ usually observed in C3 plants sometimes does not persist. Experiments were conducted to test whether the patterns of response to the environment during growth were consistent with the hypotheses that photosynthetic adjustment to elevated CO₂ concentration is due to (1) feedback inhibition or (2) nutrient stress. Soybean [*Glycine max* (L.) Merr. cv. Williams] and sugar beet (*Beta vulgaris* L. cv. Mono Hye-4) were grown from seed at 350 and 700 μmol l⁻¹ CO₂, at 20 and 25-degrees-C, at a photon flux density of 0.5 and 1.0 mmol m⁻² s⁻¹ and with three nutrient regimes until the third trifoliolate leaf of soybean or the sixth leaf of sugar beet had finished expanding. Net rates of CO₂ exchange of the most recently expanded leaves were then measured at both 350 and 700 μmol l⁻¹ CO₂. Plants grown at the elevated CO₂ concentration had net rates of leaf CO₂ exchange which were reduced by 33% in sugar beet and 23% in soybean when measured at 350 μmol l⁻¹ CO₂ and when averaged over all treatments. Negative photosynthetic adjustment to elevated CO₂ concentration was not greater at 20 than at 25-degrees-C, was not greater at a photon flux density of 1.0 than at 0.5 mmol m⁻² s⁻¹ and was not greater with limiting nutrients. Furthermore, in soybean, negative photosynthetic adjustment could be induced by a single night at elevated CO₂ concentration, with net rates of CO₂ exchange the next day equal to those of leaves of plants grown from seed at the elevated concentration of CO₂. These patterns do not support either the feedback-inhibition or the nutrient-stress hypothesis of photosynthetic adjustment to elevated concentrations of CO₂.

KEYWORDS: CO₂, COTTON, ENRICHMENT, EXCHANGE, GROWTH, LEAVES, LONG-TERM EXPOSURE, PLANTS, RESPONSES

287

Bunce, J.A. 1992. Stomatal conductance, photosynthesis and respiration of temperate deciduous tree seedlings grown outdoors at an elevated concentration of carbon-dioxide. *Plant, Cell and Environment* 15(5):541-549.

Seedlings of temperate deciduous tree species were grown outdoors at ambient and at an elevated concentration of carbon dioxide to examine how aspects of their gas exchange would be altered by growth at elevated carbon dioxide concentration. Leaf conductances to water vapour and net carbon dioxide exchange rates were determined periodically near midday. Whole-plant carbon dioxide efflux rates in darkness were also determined. The stomatal conductance of leaves of plants grown and measured at 700 μmol m⁻³ carbon dioxide did not differ from that of plants grown and measured at 350 μmol m⁻³ in *Malus domestica*, *Quercus prinus* and *Quercus robur* at any measurement time. In *Acer saccharinum*, lower conductances occurred for plants grown and measured at elevated carbon dioxide concentration only at measurement temperatures above 33-degrees-C. Photosynthetic adjustment to elevated carbon dioxide concentration was evident only in *Q. robur*. All species examined had lower rates of dark respiration per unit of mass when grown and measured at elevated carbon dioxide concentration.

KEYWORDS: CO₂ CONCENTRATION, FORESTS, RESPONSES

288

Bunce, J.A. 1993. Effects of doubled atmospheric carbon-dioxide concentration on the responses of assimilation and conductance to humidity. *Plant, Cell and Environment* 16(2):189-197.

Experiments were performed to determine if growth at elevated partial pressure of CO₂ altered the sensitivity of leaf water vapour conductance and rate of CO₂ assimilation to the leaf-to-air difference in the partial pressure of water vapour (DELTAw). Comparisons were made between plants grown and measured at 350 and 700 μPa Pa-1 partial pressures of CO₂ for amaranth, soybean and sunflower grown in controlled environment chambers, soybean grown outdoors in pots, and orchard grass grown in field plots. In amaranth, soybean and orchard grass, both the absolute and the relative sensitivity of conductance to DELTAw at the leaf surface were less in plants grown and measured at the elevated CO₂. In sunflower, there was no change in the sensitivity of conductance to DELTAw for the two CO₂ partial pressures. Tests in soybeans and amaranth showed that the change in sensitivity resulted from elevated CO₂ during the measurement of the DELTAw response. Assimilation rate of CO₂ was not altered by DELTAw in amaranth, which has C₄ metabolism. In sunflower, the assimilation rate of plants grown and measured at elevated CO₂ was insensitive to DELTAw, consistent with the response of assimilation rate to intercellular CO₂ partial pressure in the prevailing range. In soybean, the sensitivity of assimilation rate to DELTAw was not different between CO₂ treatments, in contrast to what would be expected from the response of assimilation rate to intercellular CO₂ partial pressure.

KEYWORDS: ARBUTUS-UNEDO, EFFICIENCY, LEAVES, MIDDAY DEPRESSION, NET CO₂ UPTAKE, PHOTOSYNTHETIC CAPACITY, SUNFLOWER, TRANSPIRATION, VAPOR-PRESSURE DEFICIT, WATER-STRESS

289

Bunce, J.A. 1993. Growth, survival competition, and canopy carbon-dioxide and water-vapor exchange of 1st year alfalfa at an elevated CO₂ concentration. *Photosynthetica* 29(4):557-565.

Alfalfa was grown in field plots at the current CO₂ concentration (350 μmol mol⁻¹ = c350) and at 350 μmol mol⁻¹ above the current concentration (= c700). Alfalfa and weed growth, and canopy water vapor (E) and carbon dioxide exchange (F) were determined for the first year. Alfalfa yield summed for the three harvests in the first year was greater for the c700 treatment in two of the years studied, but significantly less in a third year. Weed growth was unaffected. Survival of alfalfa plants was greater at c700 for years in which there was substantial mortality, even when yield was not increased by the c700 treatment. In spite of a persistent reduction in leaf conductance to water vapor (g(l)), total canopy conductance (g(c)) to water vapor did not differ between CO₂ treatments when averaged over years, because of compensating changes in canopy leaf area. CO₂ efflux (F) at night per unit of ground area was consistently less in the c700 treatment even when daytime CO₂ uptake was higher. Hence the periodic harvesting of alfalfa crops does not necessarily allow elevated CO₂ to cause persistent growth stimulation nor reduced water use.

KEYWORDS: ENRICHMENT, PHOTOSYNTHESIS, PLANTS, RESPIRATION, RESPONSES, TEMPERATURE, WHEAT, YIELD

290

Bunce, J.A. 1995. The effect of carbon-dioxide concentration on respiration of growing and mature soybean leaves. *Plant, Cell and Environment* 18(5):575-581.

Soybean plants were grown continuously at 350 and 700 cm³ m⁻³ CO₂ at constant temperature. Respiration rates of third trifoliolate leaves were measured at the growth CO₂ concentration for the whole dark period from 5d before through to 5d after full area expansion. The short-term response of respiration rate to the measurement CO₂ concentration was also determined at each age. Respiration rates per unit of dry mass declined with age and were significantly less at a given age or RGR in leaves grown and measured at the elevated CO₂. The difference in respiration rate was largest in mature leaves and resulted from the different measurement CO₂ concentrations. The respiratory costs of the tissue synthesis, estimated from the elemental composition of the tissue, did not differ substantially between CO₂ treatments. The response of respiration rate to carbon dioxide concentration was not strongly affected by the form of nitrogen supplied. Maintenance respiration calculated by subtracting growth respiration from total respiration was negative in rapidly growing leaves for both CO₂ treatments. This indicates that CO₂ efflux in the dark does not accurately reflect the average 24h rate of energy expenditure on growth and maintenance for soybean leaves.

KEYWORDS: CO₂-ENRICHMENT, DARK RESPIRATION, EFFLUX, ELEVATED CO₂, GROWTH, INHIBITION, MAINTENANCE, PLANT RESPIRATION, TERM

291

Bunce, J.A. 1995. Effects of elevated carbon-dioxide concentration in the dark on the growth of soybean seedlings. *Annals of Botany* 75(4):365-368.

Previous work has shown that elevated carbon dioxide (CO₂) concentrations in the dark reversibly reduce the rate of CO₂ efflux from soybeans. Experiments were performed exposing soybean plants continually to concentrations of 350 or 700 cm³ m⁻³ for 24 h d⁻¹, or to 350 during the day and 700 cm³ m⁻³ at night, in order to determine the importance of the reduced rate of dark CO₂ efflux for plant growth. High CO₂ applied only at night conserved carbon and increased dry mass during initial growth compared with the constant 350 cm³ m⁻³ treatment. Long-term net assimilation rate was increased by high CO₂ in the dark, without any increase in daytime leaf photosynthesis. However, leaf area ratio was reduced by the dark CO₂ treatment to values equal to those of plants continually exposed to the higher concentration. From days 14-21, leaf area was less for the elevated night-time CO₂ treatment than for either the constant 350 or 700 cm³ m⁻³ treatments. For the day 7-21-period, relative growth rate was significantly reduced by the high night CO₂ treatment compared with the 350 cm³ m⁻³ continuous treatment. The results indicate that some functionally significant component of respiration was reduced by the elevated CO₂ concentration in the dark.

KEYWORDS: RESPIRATION, TEMPERATURE

292

Bunce, J.A. 1995. Long-term growth of alfalfa and orchard grass plots at elevated carbon dioxide. *Journal of Biogeography* 22(2-3):341-348.

Alfalfa (*Medicago sativa* L.) and orchard grass (*Dactylis glomerata* L.) plots were exposed to ambient or ambient plus 350 cm³ m⁻³ carbon dioxide concentrations at Beltsville, Maryland, U.S.A. Replicate plots were established in different years and fertilized annually. We report here data for the second and third years after establishment. There has been no increase in the yearly production of either species at the elevated carbon dioxide concentration after the first season. In orchard grass, reduced growth at the high carbon dioxide concentration in the spring offset growth stimulation in the summer. Weed growth was consistently increased by carbon dioxide enrichment, but weed species composition was unaffected. Leaf photosynthetic capacity was reduced by the high carbon dioxide concentration in both crop species, as was leaf nitrogen

content. Canopy carbon dioxide uptake was slightly higher in the elevated carbon dioxide treatments, consistent with the increased weed growth. In alfalfa, elevated carbon dioxide significantly reduced canopy carbon dioxide efflux at night for the same daytime uptake rate and temperature. The growth conversion efficiency estimated from elemental composition of the tissue was not substantially altered by carbon dioxide treatment in either crop species, indicating little effect of carbon dioxide treatment on the respiratory cost of tissue synthesis. Canopy conductance to water vapour averaged 23% less at high than at low carbon dioxide in the orchard grass plots, and 14% less in the alfalfa plots. This was consistent with the smaller short-term response of conductance to carbon dioxide concentration in the alfalfa plots. It is concluded that a warm climate and fertile soil does not guarantee a persistent response of production to elevated carbon dioxide concentration in these herbaceous perennial species.

KEYWORDS: ATMOSPHERIC CO₂, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TRANSPIRATION, TREES

293

Bunce, J.A. 1996. Growth at elevated carbon dioxide concentration reduces hydraulic conductance in alfalfa and soybean. *Global Change Biology* 2(2):155-158.

Hydraulic conductances of alfalfa and soybean plants grown in controlled environment chambers at the current ambient carbon dioxide concentration and at twice the current ambient concentration were determined from measurements of transpiration rate and leaf and stem water potentials in the growth conditions. Growth at elevated carbon dioxide concentration reduced both transpiration rate and hydraulic conductance from the soil to the leaf in both species. Hydraulic conductance from the soil to the base of the stem was also lower at elevated carbon dioxide in soybean, but not alfalfa. These measurements identified the stem to leaf hydraulic pathway as a major target of the carbon dioxide effect in both species. The conductance of excised stem segments was much less in plants grown at elevated carbon dioxide in soybeans.

KEYWORDS: ATMOSPHERIC CO₂, WATER RELATIONS

294

Bunce, J.A. 1997. Variation in growth stimulation by elevated carbon dioxide in seedlings of some C-3 crop and weed species. *Global Change Biology* 3(1):61-66.

Seven C-3 crop and three C-3 weed species were grown from seed at 360 and at 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ carbon dioxide concentrations in a controlled environment chamber to compare dry mass, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) and photosynthetic acclimation at ambient and elevated carbon dioxide. The dry mass at the final harvest at elevated carbon dioxide relative to that at ambient carbon dioxide was highly correlated with the RGR at the lower carbon dioxide concentration. This relationship could be quite common, because it does not require that species differ in the response of RGR or photosynthesis to elevated carbon dioxide, and holds even when species differ moderately in these responses. RGR was also measured for a limited period at the end of the experiment to determine relationships with leaf gas exchange measured at this time. Relative increases in RGR at elevated carbon dioxide at this time were more highly correlated with the relative increase in NAR at elevated carbon dioxide than with the response of LAR. The amount of acclimation of photosynthesis was a good predictor of the relative increase in NAR at elevated carbon dioxide, and the longterm increase in photosynthesis in the growth environment. No differences between crops and weeds or between cool and warm climate species were found in the responses of growth or photosynthetic acclimation to elevated carbon dioxide.

KEYWORDS: CO₂- ENRICHMENT

295

Bunce, J.A. 1998. Effects of environment during growth on the sensitivity of leaf conductance to changes in humidity. *Global Change Biology* 4(3):269-274.

Soybeans (*Glycine max*) and grain amaranth (*Amaranthus hypochondriacus*) were grown at a range of temperatures, carbon dioxide concentrations and light conditions in controlled environment chambers, and the response of leaf conductance to water vapour to changes in humidity was then measured under a standard set of conditions. The sensitivity of conductance was analysed in terms of (i) the absolute sensitivity of conductance to changes in leaf to air water vapour pressure difference (LAVPD), (ii) the sensitivity of conductance relative to the absolute value of conductance, and (iii) the slope of the relationship between conductance and an index incorporating assimilation rate, carbon dioxide concentration and relative humidity. The sensitivity of conductance varied substantially with growth conditions for all three analyses in both species. The growth temperature of 25 degrees C increased the sensitivity of conductance by all three measures compared with growth at 20 or 30 degrees C in amaranth, with little difference between 25 and 30 degrees C in soybean. Growth at elevated carbon dioxide decreased sensitivity in amaranth by all three measures, and decreased the absolute but not the relative sensitivity in soybean. Growth at reduced photon flux density and growth at high stand density reduced sensitivity in amaranth by all three measures. In soybean, growth at high stand density reduced sensitivity by all three measures, but growth at low photon flux density increased the relative sensitivity. The sensitivity of leaf conductance to changes in humidity varied by a factor of two or more with growth environment by all measures of sensitivity in both the C3 and the C4 species.

KEYWORDS: C-3, CARBON DIOXIDE, CO₂, MODEL, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION

296

Bunce, J.A. 1998. The temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide in wheat and barley. *Journal of Experimental Botany* 49(326):1555-1561.

The temperature dependencies of the solubility of carbon dioxide and oxygen in water and the temperature dependency of the kinetic characteristics of the ribulose-1,5 bisphosphate carboxylase/oxygenase (Rubisco) enzyme result in the short-term stimulation of photosynthesis with a doubling of carbon dioxide from 350 to 700 $\mu\text{mol mol}^{-1}$ usually decreasing from about 90% at 30 degrees C to about 25% at 10 degrees C at high photon flux. In field-grown wheat and barley, the expected values at 30 degrees C were observed, but also values as high as 60% at 10 degrees C. The much larger than expected stimulation at cool temperatures in these species also occurred in plants grown at 15 degrees C, but not at 23 degrees C in controlled environment chambers. Gas exchange analysis indicated that an unusually high diffusive limitation was not an explanation for the large response. Assessment of the apparent in vivo specificity of Rubisco by determining the carbon dioxide concentration at which carboxylation equalled carbon dioxide release from oxygenation, indicated that growth at low temperatures altered the apparent enzyme specificity in these species compared to these species grown at the warmer temperature. Inserting the observed specificities into a biochemical model of photosynthesis indicated that altered Rubisco specificity was consistent with the observed rates of assimilation. Whether altered apparent Rubisco specificity is caused by altered stoichiometry of photorespiration or an actual change in enzyme specificity, the results indicate that the temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide may vary greatly with species and with prior exposure to low temperatures.

KEYWORDS: ASSIMILATION, CO₂/O₂ SPECIFICITY, EXCHANGE, LIGHT, PLANTS, RESPIRATION, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

297

Bunce, J.A., K.B. Wilson, and T.N. Carlson. 1997. The effect of doubled CO₂ on water use by alfalfa and orchard grass: Simulating evapotranspiration using canopy conductance measurements. *Global Change Biology* 3(1):81-87.

Alfalfa and orchard grass crops were grown at ambient and twice ambient carbon dioxide concentrations in field plots for several years in Beltsville, MD, using semiopen chambers. Canopy conductances throughout many days were determined from water vapour exchange measurements, and indicated significant reductions in canopy conductance to water vapour at elevated carbon dioxide in both species. However, recognizing that the artificial ventilation in the chambers made direct comparisons of evapotranspiration rates questionable, we used a soil-vegetation-atmosphere model to determine what field-scale evapotranspiration rates would have been with natural ventilation. Unlike the 'omega' approach, the model used allowed feedbacks between the canopy and the atmosphere, such that, for example, canopy conductance responses affected profiles of temperature and water vapour. Simulations indicated that although canopy conductances were lower at elevated carbon dioxide by as much as 20% in alfalfa and 60% in orchard grass, evapotranspiration rates never differed by more than 3% in alfalfa or 8% in orchard grass. Daily totals of evapotranspiration were only 1-2% lower at elevated carbon dioxide in alfalfa, and 2-5% lower in orchard grass. The results are partly explained by the fact that aerodynamic conductances to water vapour were generally smaller than the stomatal conductance, and also by canopy-atmosphere feedback processes which largely compensated for the lower conductance at elevated carbon dioxide by increasing the gradient for evaporation.

KEYWORDS: ASSIMILATION, CARBONDIOXIDE, ELEVATED CO₂, GROWTH, LEAF, RESPONSES, STOMATAL CONDUCTANCE, TRANSPIRATION

298

Bunce, J.A., and L.H. Ziska. 1996. Responses of respiration to increases in carbon dioxide concentration and temperature in three soybean cultivars. *Annals of Botany* 77(5):507-514.

The purpose of this experiment was to determine how respiration of soybeans may respond to potential increases in atmospheric carbon dioxide concentration and growth temperature. Three cultivars of soybeans (*Glycine max* L. Merr.), from maturity groups 00, IV, and VIII, were grown at 370, 555 and 740 cm³ m⁻³ carbon dioxide concentrations at 20/15, 25/20, and 31/26 degrees C day/night temperatures. Rates of carbon dioxide efflux in the dark were measured for whole plants several times during exponential growth. These measurements were made at the night temperature and the carbon dioxide concentration at which the plants were grown. For the lowest and highest temperature treatments, the short term response of respiration rate to measurement at the three growth carbon dioxide concentrations was also determined. Elemental analysis of the tissue was used to estimate the growth conversion efficiency. This was combined with the observed relative growth rates to estimate growth respiration. Maintenance respiration was estimated as the difference between growth respiration and total respiration. Respiration rates were generally sensitive to short term changes in the measurement carbon dioxide concentration for plants grown at the lowest, but not the highest carbon dioxide concentration. At all temperatures, growth at elevated carbon dioxide concentrations decreased total respiration measured at the growth concentration, with no significant differences among cultivars. Total respiration increased very little with increasing growth

temperature, despite an increase in relative growth rate. Growth respiration was not affected by carbon dioxide treatment at any temperature, but increased with temperature because of the increase in relative growth rate. Values calculated for maintenance respiration decreased with increasing carbon dioxide concentration and also decreased with increasing temperature. Calculated values of maintenance respiration were sometimes zero or negative at the warmer temperatures. This suggests that respiration rates measured in the dark may not have reflected average 24-h rates of energy use. The results indicate that increasing atmospheric carbon dioxide concentration may reduce respiration in soybeans, and respiration may be insensitive to climate warming. (C) 1996 Annals of Botany Company

KEYWORDS: EFFLUX, ELEVATED CO₂, ENRICHMENT, GROWTH, INHIBITION, LEAVES, MAINTENANCE REQUIREMENTS, PHOTOSYNTHESIS, PLANT RESPIRATION, WHITE CLOVER

299

Bunce, J.A., and L.H. Ziska. 1998. Decreased hydraulic conductance in plants at elevated carbon dioxide. *Plant, Cell and Environment* 21(1):121-126.

Previous work indicated that long-term exposure to elevated carbon dioxide levels can reduce hydraulic conductance in some species, but the basis of the response was not determined. In this study, hydraulic conductance was measured at concentrations of both 350 and 700 cm³ m⁻³ carbon dioxide for plants grown at both concentrations, to determine the reversibility of the response. In *Zea mays* and *Amaranthus hypochondriacus*, exposure to the higher carbon dioxide concentration for several hours reduced whole-plant transpiration rate by 22-40%, without any consistent change in leaf water potential, indicating reversible reductions in hydraulic conductance at elevated carbon dioxide levels. Hydraulic conductance in these species grown at both carbon dioxide concentrations responded similarly to measurement concentration of carbon dioxide, indicating that the response was reversible. In *Glycine max*, which in earlier work had shown a long-term decrease in hydraulic conductance at elevated carbon dioxide levels, and in *Abutilon theophrasti*, no short-term changes in hydraulic conductance with measurement concentration of carbon dioxide were found, despite lower transpiration rates at elevated carbon dioxide. In *G. max* and *Medicago sativa*, growth at high dew-point temperature reduced transpiration rate and decreased hydraulic conductance. The results indicate that both reversible and irreversible decreases in hydraulic conductance can occur at elevated carbon dioxide concentrations, and that both could be responses to reduced transpiration rate, rather than to carbon dioxide concentration itself.

KEYWORDS: ATMOSPHERIC CO₂, CONDUCTIVITY, COTTON PLANTS, ENRICHMENT, GRASSLAND, GROWTH, RESISTANCE, STRESS, WATER TRANSPORT, YIELD

300

Burton, A.J., G.P. Zogg, K.S. Pregitzer, and D.R. Zak. 1997. Effect of measurement CO₂ concentration on sugar maple root respiration. *Tree Physiology* 17(7):421-427.

Accurate estimates of root respiration are crucial to predicting belowground C cycling in forest ecosystems. Inhibition of respiration has been reported as a short-term response of plant tissue to elevated measurement [CO₂]. We sought to determine if measurement [CO₂] affected root respiration in samples from mature sugar maple (*Acer saccharum* Marsh.) forests and to assess possible errors associated with root respiration measurements made at [CO₂]s lower than that typical of the soil atmosphere. Root respiration was measured as both CO₂ production and O₂ consumption on excised fine roots (less than or equal to 1.0 mm) at [CO₂]s ranging from 350 to > 20,000 μl l⁻¹.

Root respiration was significantly affected by the [CO₂] at which measurements were made for both CO₂ production and O₂ consumption. Root respiration was most sensitive to [CO₂] near and below normal soil concentrations (< 1500 μmol l⁻¹). Respiration rates changed little at [CO₂]s above 3000 μmol l⁻¹ and were essentially constant above 6000 μmol l⁻¹ CO₂. These findings call into question estimates of root respiration made at or near atmospheric [CO₂], suggesting that they overestimate actual rates in the soil. Our results indicate that sugar maple root respiration at atmospheric [CO₂] (350 μmol l⁻¹) is about 139% of that at soil [CO₂]. Although the causal mechanism remains unknown, the increase in root respiration at low measurement [CO₂] is significant and should be accounted for when estimating or modeling root respiration. Until the direct effect of [CO₂] on root respiration is fully understood, we recommend making measurements at a [CO₂] representative of, or higher than, soil [CO₂]. In all cases, the [CO₂] at which measurements are made and the [CO₂] typical of the soil atmosphere should be reported.

KEYWORDS: CARBON-DIOXIDE CONCENTRATIONS, ENRICHMENT, FOREST ECOSYSTEMS, HIGHER-PLANTS, INTRACELLULAR PH, MAINTENANCE RESPIRATION, PINE PLANTATIONS, SHORT- TERM, SOIL O₂, TEMPERATURE

301

Burton, P.J., and S.G. Cumming. 1995. Potential effects of climatic-change on some western canadian forests, based on phenological enhancements to a patch model of forest succession. *Water, Air, and Soil Pollution* 82(1-2):401-414.

We enhanced the forest patch model, Zelig, to explore the implications of 2xCO₂ climate change scenarios on several forest regions in British Columbia and Alberta, Canada. In addition to the processes and phenomena commonly represented in individual-based models of forest stand dynamics, we added some species-specific phenology and site-specific frost events. The consideration of bud-break heat sum requirements, growing season limits, and chilling requirements for the induction of dormancy and cold hardiness slightly improved the ability of Zelig to predict the present composition of B.C. forests. Simulations of the predicted effects of future climatic regimes (based on the averaged predictions of four general circulation models) include some major shifts in equilibrium, forest composition and productivity. Lowland temperate coastal forests are predicted to be severely stressed because indigenous species will no longer have their winter chilling requirements met. High-elevation coastal forests are expected to increase in productivity, while interior subalpine forests are expected to remain stable in productivity but will gradually be replaced by species currently characteristic of lower elevations. Dry, interior low-elevation forests in southern B.C. are likely to persist relatively unchanged, while wet interior forests are expected to support dramatic increases in yield, primarily by western hemlock. Northern interior sub-boreal forests are likewise expected to increase in productivity through enhanced growth of lodgepole pine. Conversely, the precipitous collapse of spruce stands in the true boreal forests of northeastern B.C. is expected to be associated with reduced productivity as they are replaced by pine species. Boreal-Cordilleran and Moist Boreal Mixedwood forests in Alberta are less likely to undergo compositional change, while becoming somewhat more productive. We believe these model enhancements to be a significant improvement over existing formulations, but the resulting predictions must still be viewed with caution. Model limitations include: (1) the current inability of climate models to predict future variation in monthly temperature and precipitation; (2) sparse information on the phenological behaviour of several important tree species; and (3) a poor understanding of the degree to which growth is constrained by different suboptimal climatic events.

KEYWORDS: BUDBURST, CARBON, CO₂, FREEZING RESISTANCE, GLOBAL CLIMATE, SCALE, SENSITIVITY, TREES

302

Buse, A., and J.E.G. Good. 1996. Synchronization of larval emergence in winter moth (*Operophtera brumata* L) and budburst in pedunculate oak (*Quercus robur* L) under simulated climate change. *Ecological Entomology* 21(4):335-343.

1. The hypothesis that a 3 degrees C elevation in temperature and doubled CO₂ concentration would have no effect on the synchronization of winter moth egg hatch with budburst in oak was tested by comparing the separate and interactive effects of ambient and elevated (+ 3 degrees C) temperature and ambient and elevated (doubled to 340 p.p.m.) CO₂ in eight experimental Solardomes. In addition, an outdoor control was compared with the ambient temperature/CO₂ treatment combination. 2. Elevated temperature accelerated darkening (preceding egg hatch by about 5-10 days) and hatching of eggs developing off the trees; elevated CO₂ had no effect. The same effects were observed in eggs developing on the trees. 3. Within treatments, date of egg hatch was the same on trees with early or late budburst. 4. Egg darkening and budburst were closely synchronized at both ambient and elevated temperatures. 5. Both eggs and trees required fewer cumulative heat units (day degrees > 4 degrees C), for hatching and budburst, respectively, at ambient than elevated temperatures. The requirements in the outdoor control treatment were similar to those in the ambient Solardome treatment. 6. Egg hatch between 10 and 25 degrees C, on a temperature gradient in the laboratory, required a constant number of heat units; fewer were required below 10 degrees C. 7. Elevated temperatures, in the Solardomes and the field, delayed adult emergence from the pupae. 8. The results suggest that a general increase in temperature with climatic change would not affect the closeness of the synchronization between egg hatch of winter moth and budburst of oak.

KEYWORDS: BRITAIN, GEOMETRIDAE, LEPIDOPTERA, OUTBREAKS, SCOTLAND, SITKA SPRUCE, TEMPERATURE, TREES

303

Buse, A., J.E.G. Good, S. Dury, and C.M. Perrins. 1998. Effects of elevated temperature and carbon dioxide on the nutritional quality of leaves of oak (*Quercus robur* L.) as food for the Winter Moth (*Operophtera brumata* L.). *Functional Ecology* 12(5):742-749.

1. Pedunculate Oak trees were grown in ambient and elevated temperatures and CO₂. Leaves were fed to Winter Moth caterpillars reared either in constant conditions or with the trees (caged or on-tree). 2. Caterpillars in constant conditions ate the same mass and produced the same mass of faeces whether fed elevated or ambient temperature leaves. However, less was assimilated from elevated leaves, resulting in lighter pupae and fewer, lighter eggs. 3. Caterpillars in constant conditions ate more and produced more faeces when fed elevated CO₂ leaves than when fed ambient CO₂ leaves, but the mass assimilated and pupal mass were unchanged. 4. Caged caterpillars reared with the trees from which they were fed had constant pupal mass in all treatments, but pupated earlier at elevated temperature. Pupal mass was also unaffected when caterpillars fed on the trees. 5. Nitrogen was reduced in both elevated temperature and elevated CO₂ leaves. Increased fibre in the former prevented increased consumption and resulted in reduced pupal mass and fecundity. Reduced fibre in the latter allowed increased consumption, resulting in pupae of normal mass. 6. Despite the clear effect of nutrient quality, experiments rearing caterpillars and trees together suggest that anticipated climatic change will have no nutritional effect on Winter Moth development.

KEYWORDS: ATMOSPHERIC CO₂, DECIDUOUS TREES, FEEDING RESPONSE, GROWTH, HERBIVORE INTERACTIONS, HOST PLANTS, INSECT PERFORMANCE, LYMANTRIA-DISPAR, NITROGEN, PLANT-RESPONSES

304

Bytnerowicz, A. 1996. Physiological aspects of air pollution stress in forests. *Phyton-Annales Rei Botanicae* 36(3):15-22.

Air pollutants, such as ozone, sulfur dioxide, nitrogen compounds and others, affect health of forests in Europe and North America. Gaseous air pollutants enter plants mainly through stomata, although transcuticular transport can also be important for some pollutants. Toxic effects of pollutants depend on their effective dose that is proportional to pollutant ambient concentration and plant stomatal conductance. Mechanisms of air pollution toxicity are very complex and depend on various physiological and biochemical properties of plants. These mechanisms (including formation of free radicals) are still poorly understood. In addition, physiological responses of forest plants to air pollution stress can be modified by various biotic (e.g., insects, pathogens, mycorrhizae associations, genetic variation) and abiotic (e.g., increasing CO₂ concentrations, ultraviolet-B radiation, nitrogen deposition, nutrient deficiencies, drought) factors. An example of air pollution effects on forest trees may be responses of ponderosa pine seedlings to elevated concentrations of ozone in the Sierra Nevada. Various physiological changes caused by ozone (e.g., lowered net photosynthesis, altered carbon allocation, deterioration of photosynthetic pigments, etc.) have led to the reduced growth and biomass of the seedlings.

KEYWORDS: ATMOSPHERIC OZONE, B RADIATION, NITROGEN, PINE, SULFUR, VEGETATION

305

Cairney, J.W.G., and A.A. Meharg. 1999. Influences of anthropogenic pollution on mycorrhizal fungal communities. *Environmental Pollution* 106(2):169-182.

Mycorrhizal fungi form complex communities in the root systems of most plant species and are thought to be important in terrestrial ecosystem sustainability. We have reviewed the literature relating to the influence of the major forms of anthropogenic pollution on the structure and dynamics of mycorrhizal fungal communities. All forms of pollution have been reported to alter the structure of below-ground communities of mycorrhizal fungi to some degree, although the extent to which such changes will be sustained in the longer term is at present not clear. The major limitation to predicting the consequences of pollution-mediated changes in mycorrhizal fungal communities to terrestrial habitats is our limited understanding of the functional significance of mycorrhizal fungal diversity. While this is identified as a priority area for future research, it is suggested that, in the absence of such data, an understanding of pollution-mediated changes in mycorrhizal mycelial systems in soil may provide useful indicators for sustainability of mycorrhizal systems. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ABIES L KARST, ELEVATED ATMOSPHERIC CO₂, LANDFILL SITE RESTORATION, LOBLOLLY-PINE SEEDLINGS, NORWAY SPRUCE, RED SPRUCE SEEDLINGS, SCOTS PINE, SIMULATED ACID-RAIN, TAEDA L SEEDLINGS, VESICULAR-ARBUSCULAR MYCORRHIZAE

306

Callaway, R.M., E.H. Delucia, E.M. Thomas, and W.H. Schlesinger. 1994. Compensatory responses of CO₂ exchange and biomass allocation and their effects on the relative growth-rate of ponderosa pine in different CO₂ and temperature regimes. *Oecologia* 98(2):159-166.

Increases in the concentration of atmospheric carbon dioxide may have a fertilizing effect on plant growth by increasing photosynthetic rates and therefore may offset potential growth decreases caused by the stress associated with higher temperatures and lower precipitation. However, plant growth is determined both by rates of net photosynthesis and by

proportional allocation of fixed carbon to autotrophic tissue and heterotrophic tissue. Although CO₂ fertilization may enhance growth by increasing leaf-level assimilation rates, reallocation of biomass from leaves to stems and roots in response to higher concentrations of CO₂ and higher temperatures may reduce whole-plant assimilation and offset photosynthetic gains. We measured growth parameters, photosynthesis, respiration, and biomass allocation of *Pinus ponderosa* seedlings grown for 2 months in 2 x 2 factorial treatments of 350 or 650 μm bar CO₂ and 10/25-degrees-C or 15/30-degrees-C night/day temperatures. After 1 month in treatment conditions, total seedling biomass was higher in elevated CO₂, and temperature significantly enhanced the positive CO₂ effect. However, after 2 months the effect of CO₂ on total biomass decreased and relative growth rates did not differ among CO₂ and temperature treatments over the 2-month growth period even though photosynthetic rates increased almost-equal-to 7% in high CO₂ treatments and decreased almost-equal-to 10% in high temperature treatments. Additionally, CO₂ enhancement decreased root respiration and high temperatures increased shoot respiration. Based on CO₂ exchange rates, CO₂ fertilization should have increased relative growth rates (RGR) and high temperatures should have decreased RGR. Higher photosynthetic rates caused by CO₂ fertilization appear to have been mitigated during the second month of exposure to treatment conditions by a almost-equal-to 3% decrease in allocation of biomass to leaves and a almost-equal-to 9% increase in root:shoot ratio. It was not clear why diminished photosynthetic rates and increased respiration rates at high temperatures did not result in lower RGR. Significant diametrical and potentially compensatory responses of CO₂ exchange and biomass allocation and the lack of differences in RGR of ponderosa pine after 2 months of exposure of high CO₂ indicate that the effects of CO₂ fertilization and temperature on whole-plant growth are determined by complex shifts in biomass allocation and gas exchange that may, for some species, maintain constant growth rates as climate and atmospheric CO₂ concentrations change. These complex responses must be considered together to predict plant growth reactions to global atmospheric change, and the potential of forest ecosystems to sequester larger amounts of carbon in the future.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GREAT-BASIN, LEAF-AREA, RESPIRATION, SEEDLINGS, SOIL, VEGETATION, WATER-USE EFFICIENCY, WOODY-PLANTS

307

Campbell, B.D., W.A. Laing, D.H. Greer, J.R. Crush, H. Clark, D.Y. Williamson, and M.D.J. Given. 1995. Variation in grassland populations and species and the implications for community responses to elevated CO₂. *Journal of Biogeography* 22(2-3):315-322.

Variation in plant characteristics and potential responses to CO₂ was measured in controlled environments for a set of different forage plant species and populations. The response of the plants to elevated CO₂ was strongly determined by temperature. The greatest responses to elevated CO₂ were observed at warm temperatures in C3 species with high potential growth rates at these temperatures. This suggests that the community composition could change most rapidly in response to CO₂ in warm seasons, with the greatest positive responses to CO₂ occurring in warm-season active species. This prediction was tested in a microcosm experiment. The prediction was confirmed under well-watered conditions but water stress resulted in an ingress of C4 species with low potential responses to CO₂. The results suggest that variation between populations and species must be considered when predicting grassland community responses to CO₂, and that it is inappropriate to ignore compositional changes in communities when modelling CO₂ effects on pasture production. Given the importance of temperature in determining CO₂ responsiveness, phenology may prove to be a useful attribute in plant functional type analyses of community responses to CO₂.

KEYWORDS: ENRICHMENT

308

Campbell, B.D., D.M.S. Smith, and G.M. McKeon. 1997. Elevated CO₂ and water supply interactions in grasslands: A pastures and rangelands management perspective. *Global Change Biology* 3(3):177-187.

Water is a key variable driving the composition and productivity of pastures and rangelands, and many of the ecosystems in these grasslands are highly sensitive to changes in water supply. The possibility that elevated CO₂ concentrations may alter plant water relations is therefore particularly relevant to pastures and rangelands, and may have important consequences for grassland ecosystem function, water use, carbon storage and nutrient cycling. The planning of effective research to better understand these changes requires attention to both: (i) gaps in knowledge about CO₂ and water interactions, and (ii) knowledge of how precisely the effects of CO₂ must be understood in relation to other factors, in order to predict changes in grassland structure and production. A recent microcosm experiment illustrates that non-linear effects of CO₂ and water stress could perturb primary production by triggering changes in grassland community composition. The magnitudes of the effects of CO₂ on key grassland ecosystems remain to be precisely determined through ecosystem-level experiments. A simplified simulation of the impact of different levels of productivity change in a water-limited Australian rangeland system was conducted by varying effects of CO₂ on radiation and water use efficiency. The results indicate that direct effects of CO₂ may be moderated at the enterprise scale by accompanying changes in adaptive management by farmers. We conclude that future research should aim to construct quantitative relationships and identify thresholds of response for different grassland systems. The sensitivity of these systems to management (such as grazing pressure) should also be considered when developing integrated predictions of future effects of CO₂ on water supply to grassland ecosystems.

KEYWORDS: DESERT ECOSYSTEMS, TALLGRASS PRAIRIE, UNITED-STATES

309

Campbell, W.J. 1997. Intraspecific variation of rubisco and rubisco activase protein levels in tomato leaves grown at elevated CO₂ concentration. *Plant Physiology* 114(3):1056.

310

Canadell, J.G., L.F. Pitelka, and J.S.I. Ingram. 1996. The effects of elevated [CO₂] on plant-soil carbon below-ground: A summary and synthesis. *Plant and Soil* 187(2):391-400.

We undertake a synthesis of the most relevant results from the presentations at the meeting "Plant-Soil Carbon Below-Ground: The Effects of Elevated CO₂" (Oxford-UK, September 1995), many of which are published in this Special Issue. Below-ground responses to elevated [CO₂] are important because the capacity of soils for long-term carbon sequestration. We draw the following conclusions: (i) several ecosystems exposed to elevated [CO₂] showed sustained increased CO₂ uptake at the plot level for many years. A few systems, however, showed complete down-regulation of net CO₂ uptake after several years of elevated [CO₂] exposure; (ii) under elevated [CO₂], a greater proportion of fixed carbon is generally allocated below-ground, potentially increasing the capacity of below-ground sinks; and (iii) some of the increased capacity of these sinks may lead to increased long-term soil carbon sequestration, although strong evidence is still lacking. We highlight the need for more soil studies to be undertaken within ongoing ecosystem-level

experiments, and suggest that while some key experiments already established should be maintained to allow long term effects and feedbacks to take place, more research effort should be directed to mechanisms of soil organic matter stabilization.

KEYWORDS: DIOXIDE, ECOSYSTEMS, GAS-EXCHANGE, GRASSLAND, INCREASING ATMOSPHERIC CO₂, NITROGEN, ORGANIC-MATTER, PHOTOSYNTHESIS, RESPONSES, TURNOVER

311

Cannell, M.G.R., and J.H.M. Thornley. 1998. N-poor ecosystems may respond more to elevated [CO₂] than N-rich ones in the long term. A model analysis of grassland. *Global Change Biology* 4(4):431-442.

The Hurley Pasture Model was used to examine the short and long-term responses of grazed grasslands in the British uplands to a step increase from 350 to 700 $\mu\text{mol mol}^{-1}$ CO₂ concentration ([CO₂]) with inputs of 5 or 100 kg N ha⁻¹ y⁻¹. In N-rich grassland, [CO₂] doubling quickly increased net primary productivity (NPP), total carbon (C-sys) and plant biomass by about 30%. By contrast, the N-poor grassland underwent a prolonged 'transient', when there was little response, but eventually NPP, C-sys and plant biomass more than doubled. The 'transient' was due to N immobilization and severe depletion of the soil mineral N pool. The large long-term response was due to slow N accumulation, as a result of decreased leaching, decreased gaseous N losses and increased N₂-fixation, which amplified the CO₂ response much more in the N-poor than in the N-rich grassland. It was concluded that (i) ecosystems use extra carbon fixed at high [CO₂] to acquire and retain nutrients, supporting the contention of Gifford et al. (1996), (ii) in the long term, and perhaps on the real timescale of increasing [CO₂], the response (in NPP, C-sys and plant biomass) of nutrient-poor ecosystems may be proportionately greater than that of nutrient-rich ones, (iii) short-term experiments on nutrient-poor ecosystems may observe only the transient responses, (iv) the speed of ecosystem responses may be limited by the rate of nutrient accumulation rather than by internal rate constants, and (v) ecosystem models must represent processes affecting nutrient acquisition and retention to be able to simulate likely real-world CO₂ responses.

KEYWORDS: ATMOSPHERIC CO₂, DIOXIDE, ENRICHMENT, FOREST ECOSYSTEMS, GAS-EXCHANGE, GLOBAL CARBON-CYCLE, GROWTH-RESPONSES, PLANT-RESPONSES, ROOT-GROWTH, TERRESTRIAL ECOSYSTEMS

312

Cannell, M.G.R., and J.H.M. Thornley. 1998. Temperature and CO₂ responses of leaf and canopy photosynthesis: A clarification using the non-rectangular hyperbola model of photosynthesis. *Annals of Botany* 82(6):883-892.

The responses of C-3 leaf and canopy gross photosynthesis to increasing temperature and CO₂ can be readily understood in terms of the temperature and CO₂ dependencies of quantum yield ($\phi(i)$) and light-saturated photosynthesis ($A(\text{sat})$) the two principal parameters in the non-rectangular hyperbola model of photosynthesis. Here, we define these dependencies within the mid-range for C-3 herbaceous plants, based on a review of the literature. Then, using illustrative parameter values, we deduce leaf and canopy photosynthesis responses to temperature and CO₂ in different environmental conditions (including shifts in the temperature optimum) from the assumed sensitivities of $\phi(i)$ and $A(\text{sat})$ to temperature and CO₂. We show that: (1) elevated CO₂ increases photosynthesis more at warm than at cool temperatures because of the large combined CO₂-responses of both $\phi(i)$ and $A(\text{sat})$ at high temperatures; (2) elevated CO₂ may substantially raise the temperature optimum of photosynthesis at warm temperatures, but not at the cool temperatures which prevail for much of the time at temperate

and high latitudes; (3) large upward shifts in the temperature optimum of canopy gross photosynthesis occur at high irradiances, following the response of A(sat), and are probably important for global carbon fixation; (4) canopy gross photosynthesis shows smaller CO₂-temperature interactions than leaf photosynthesis, because leaves in canopies receive lower average irradiances and sep more strongly follow the dependencies of phi(i); and (5) at very low irradiances, the temperature optimum of photosynthesis is low and is raised very little by increasing CO₂. (C) 1998 Annals of Botany Company.

KEYWORDS: C-4 PLANTS, CARBON DIOXIDE, CARBOXYLASE-OXYGENASE, CHLOROPHYLL FLUORESCENCE, CLIMATE CHANGE, DEPENDENCE, EUCALYPTUS-PAUCIFLORA, LIGHT, QUANTUM YIELDS, VASCULAR PLANTS

313

Cannon, R.J.C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* 4(7):785-796.

Recent estimates for global warming predict increases in global mean surface air temperatures (relative to 1990) of between 1 and 3.5 degrees C, by 2100. The impact of such changes on agricultural systems in mid- to high-latitude regions are predicted to be less severe than in low-latitude regions, and possibly even beneficial, although the influence of pests and diseases is rarely taken into account. Most studies have concluded that insect pests will generally become more abundant as temperatures increase, through a number of inter-related processes, including range extensions and phenological changes, as well as increased rates of population development, growth, migration and overwintering. A gradual, continuing rise in atmospheric CO₂ will affect pest species directly (i.e. the CO₂ fertilization effect) and indirectly (via interactions with other environmental variables). However, individual species responses to elevated CO₂ vary: consumption rates of insect herbivores generally increase, but this does not necessarily compensate fully for reduced leaf nitrogen. The consequent effects on performance are strongly mediated via the host species. Some recent experiments under elevated CO₂ have suggested that aphids may become more serious pests, although other studies have discerned no significant effects on sap-feeding homopterans. However, few, if any of these experiments have fully considered the effects on pest population dynamics. Climate change is also considered from the perspective of changes in the distribution and abundance of species and communities. Marked changes in the distribution of well-documented species - including Odonata, Orthoptera and Lepidoptera - in northwestern Europe, in response to unusually hot summers, provide useful indications of the potential effects of climate change. Migrant pests are expected to respond more quickly to climate change than plants, and may be able to colonize newly available crops/habitats. Range expansions, and the removal of edge effects, could result in the increased abundance of species presently near the northern limits of their ranges in the UK. However, barriers to range expansions, or shifts, may include biotic (competition, predation, parasitism and disease), as well as abiotic, factors. Climatic phenomena, ecosystem processes and human activities are interactive and interdependent, making long-term predictions extremely tenuous. Nevertheless, it appears prudent to prepare for the possibility of increases in the diversity and abundance of pest species in the UK, in the context of climate change.

KEYWORDS: BRITISH BUTTERFLY FAUNA, CARBON-DIOXIDE ATMOSPHERES, DECIDUOUS TREES, ELEVATED CO₂, ENRICHED CO₂ ATMOSPHERES, GLOBAL CHANGE, HERBIVORE INTERACTIONS, JUNONIA-COENIA, LARVAL EMERGENCE, POPULATION-DYNAMICS

314

Cantin, D., M.F. Tremblay, M.J. Lechowicz, and C. Potvin. 1997. Effects of CO₂ enrichment, elevated temperature, and nitrogen availability on the growth and gas exchange of different families of jack pine seedlings. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 27(4):510-520.

Many economically important tree species respond positively to an elevated CO₂ environment. However, the variability and stability in growth responses among genotypes grown in a global change environment are generally not documented. The present study investigated the differences, at the seedling stage, among 15 maternal families of jack pine (*Pinus banksiana* Lamb.) in response to an elevated CO₂-temperature environment (CO₂T) (700 mu L CO₂.L-1 with temperatures 4 degrees C higher than in the ambient CO₂T environment), with different nitrogen concentrations. While the elevated CO₂T did not significantly alter the overall height growth of seedlings, it significantly increased their total biomass, with needle and root biomass being most responsive. Growth in the elevated CO₂T resulted in a 24% reduction in the leaf weight ratio as more biomass was allocated to roots. Significant genotypic differences were observed for height, biomass, and water-use efficiency. Generally, most families kept their rank relative to other families, from the ambient to the elevated CO₂T. Also, rank correlations between height of families grown in elevated CO₂T and height of families at 10 years of age in the field were significant. This result, combined with the stability we observed in family response from the ambient to the elevated CO₂T, suggested that jack pine families currently chosen for their fast-growing capacity will probably remain as such in a global change environment, at least during the seedling establishment stage.

KEYWORDS: AGE-AGE CORRELATIONS, ATMOSPHERIC CO₂, BLACK SPRUCE SEEDLINGS, CLIMATE CHANGE, EARLY SELECTION, PATTERNS, PHENOTYPIC PLASTICITY, PICEA MARIANA, RESPONSES, X ENVIRONMENT INTERACTIONS

315

Cao, M.K., and F.I. Woodward. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Global Change Biology* 4(2):185-198.

Evaluating the role of terrestrial ecosystems in the global carbon cycle requires a detailed understanding of carbon exchange between vegetation, soil, and the atmosphere. Global climatic change may modify the net carbon balance of terrestrial ecosystems, causing feedbacks on atmospheric CO₂ and climate. We describe a model for investigating terrestrial carbon exchange and its response to climatic variation based on the processes of plant photosynthesis, carbon allocation, litter production, and soil organic carbon decomposition. The model is used to produce geographical patterns of net primary production (NPP), carbon stocks in vegetation and soils, and the seasonal variations in net ecosystem production (NEP) under both contemporary and future climates. For contemporary climate, the estimated global NPP is 57.0 Gt C y⁻¹, carbon stocks in vegetation and soils are 640 Gt C and 1358 Gt C, respectively, and NEP varies from -0.5 Gt C in October to 1.6 Gt C in July. For a doubled atmospheric CO₂ concentration and the corresponding climate, we predict that global NPP will rise to 69.6 Gt C y⁻¹, carbon stocks in vegetation and soils will increase by, respectively, 133 Gt C and 160 Gt C, and the seasonal amplitude of NEP will increase by 76%. A doubling of atmospheric CO₂ without climate change may enhance NPP by 25% and result in a substantial increase in carbon stocks in vegetation and soils. Climate change without CO₂ elevation will reduce the global NPP and soil carbon stocks, but leads to an increase in vegetation carbon because of a forest extension and NPP enhancement in the north. By combining the effects of CO₂ doubling, climate change, and the consequent redistribution of vegetation, we predict a strong enhancement in NPP and carbon stocks of terrestrial ecosystems. This study simulates the possible variation in the carbon

exchange at equilibrium state. We anticipate to investigate the dynamic responses in the carbon exchange to atmospheric CO₂ elevation and climate change in the past and future.

KEYWORDS: ATMOSPHERIC CO₂, DECOMPOSITION, DYNAMICS, FOREST ECOSYSTEMS, GLOBAL-MODEL, PHOTOSYNTHESIS, PLANT, SIMULATION, SINK, SOIL

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Cao, W.X., and T.W. Tibbitts. 1997. Starch concentration and impact on specific leaf weight and element concentrations in potato leaves under varied carbon dioxide and temperature. *Journal of Plant Nutrition* 20(7-8):871-881.

Foliar concentrations of starch and major elements, nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), along with specific leaf weight (SLW) were determined in the potato (*Solanum tuberosum* L.) cvs 'Denali', 'Norland', and 'Russet Burbank' grown for 35 days under CO₂ concentrations of 500, 1,000, 1,500 and 2,000 $\mu\text{mol} \cdot \text{mol}^{-1}$ at both 16 degrees C and 20 degrees C air temperature. The starch concentration, pooled from the three cultivars, increased with increasing CO₂ concentration at both 16 degrees C and 20 degrees C and was consistently higher at 16 degrees C than at 20 degrees C. The SLW ($\text{g} \cdot \text{m}^{-2}$) was positively related to the foliar starch concentration on the basis of leaf area or dry weight. The concentrations of N, P, Ca, and Mg in leaves were negatively related to starch concentration under approximate to 14% starch on a dry weight basis. Above 14% starch, there was no significant relationship between element and starch concentrations. Similar patterns were seen when the SLW and element concentrations were expressed on a starch-free basis. In contrast, the leaf concentration of K was not closely related to the starch concentration because the K concentration was similar at varied CO₂ levels. The results of this study indicate that the changes in SLW and concentrations of N, P, Ca, and Mg in potato leaves only partially resulted from the changed starch concentration.

KEYWORDS: CO₂- ENRICHMENT, GROWTH, LIFE SUPPORT SYSTEMS, NITROGEN, PHOTOPERIODS, RESPONSES, WHEAT

317

Cao, W., T.W. Tibbitts, and R.M. Wheeler. 1994. Carbon-dioxide interactions with irradiance and temperature in potatoes. *Life Sciences and Space Research XXV (3) 14(11):243-250.*

Separate controlled environment studies were conducted to determine the interaction of CO₂ with irradiance and interaction of CO₂ with temperature on growth of three potato cultivars. In the first study, an elevated CO₂ concentration of 1000 $\mu\text{mol} \cdot \text{mol}^{-1}$ and an ambient CO₂ of 350 $\mu\text{mol} \cdot \text{mol}^{-1}$ were maintained at the photosynthetic photon fluxes (PPF) of 17 and 34 $\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ with 12 h photoperiod, and at the PPF of 34 and 68 $\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ with 24 h photoperiod (400 and 800 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PPF at each photoperiod). Tuber and total dry weights of 90-day old potatoes were significantly increased with CO₂ enrichment, but the CO₂ stimulation was less with higher PPF and longer photoperiod. Shoot dry weight was affected more by photoperiod than by PPF and CO₂ concentrations. The elevated CO₂ concentration increased leaf CO₂ assimilation rates and decreased stomatal conductance with 12 h photoperiod, but had only a marginal effect with 24 h photoperiod. In the second study, four CO₂ concentrations of 500, 1000, 1500 and 2000 $\mu\text{mol} \cdot \text{mol}^{-1}$ were combined with two air temperature regimes of 16 and 20 degrees C under a 12 h photoperiod. At harvest, 35 days after transplanting, tuber and total dry weights of potatoes reached a maximum with 1000 $\mu\text{mol} \cdot \text{mol}^{-1}$ CO₂ at 16 degrees C, but continued to increase up to 2000 $\mu\text{mol} \cdot \text{mol}^{-1}$ CO₂ at 20 degrees C. Plant growth was greater at 20 degrees C than at 16 degrees C under all CO₂ concentrations. At 16

degrees C specific leaf weight increased substantially with increasing CO₂ concentrations as compared to 500 $\mu\text{mol} \cdot \text{mol}^{-1}$ CO₂, but increased only slightly at 20 degrees C. This suggests a carbohydrate build-up in the leaves at 16 degrees C temperature that reduces plant response to increased CO₂ concentrations. The data in the two studies indicate that a PPF of 34 $\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, 20 degrees C temperature, and 1000-2000 $\mu\text{mol} \cdot \text{mol}^{-1}$ CO₂ produces optimal tuber yield in potatoes.

KEYWORDS: 24-H, CO₂- ENRICHMENT, GROWTH, LIFE SUPPORT SYSTEMS, PHOTOPERIODS, PHOTOSYNTHESIS, PLANTS, RESPONSES, SOLANUM-TUBEROSUM, SPACE

318

Caporn, S.J.M., A.L. Brooks, M.C. Press, and J.A. Lee. 1999. Effects of long-term exposure to elevated CO₂ and increased nutrient supply on bracken (*Pteridium aquilinum*). *Functional Ecology* 13:107-115.

1. Bracken (*Pteridium aquilinum*) is an important fern with a global distribution. Little is known of the response of this species to elevated CO₂. We investigated the effects of high CO₂ (570 compared with 370 $\mu\text{mol} \cdot \text{mol}^{-1}$) with and without an increased nutrient supply (a combined N, P, K application) on the growth and physiology of bracken, growing in containers in controlled-environment glasshouses, over two full growing seasons. Results of growth and physiology determinations are reported for the second season. 2. Elevated CO₂ had little impact on the growth or allocation of dry mass in bracken. No significant changes were detected in dry mass of the total plant or any of the organs: rhizomes, roots and fronds. In contrast to the small effects of high CO₂ the high nutrient treatment caused a three-fold stimulation of total plant dry mass and an increase in the allocation of dry mass to above ground when compared with low nutrient controls. 3. Net photosynthetic rates in saturating light were increased by both high CO₂ and nutrient treatments, particularly in spring months (May and June). Growth in elevated CO₂ did not cause a down-regulation in light-saturated rates of photosynthesis. The increased carbon gain in the high CO₂ treatments was accompanied, in the low-nutrient plants, by higher concentrations of carbohydrates. However, in high-nutrient plants the CO₂ treatment did not cause an accumulation of carbohydrates. The absence of a growth response to elevated CO₂ in bracken despite significant increases in photosynthesis requires further investigation.

KEYWORDS: ENGLAND, GROWTH, MANAGEMENT, NITROGEN, PHOTOSYNTHESIS

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Caporn, S.J.M., D.W. Hand, T.A. Mansfield, and A.R. Wellburn. 1994. Canopy photosynthesis of CO₂-enriched lettuce (*Lactuca sativa* L.) - response to short-term changes in CO₂, temperature and oxides of nitrogen. *New Phytologist* 126(1):45-52.

The canopy net photosynthesis (P_n) of lettuce (*Lactuca sativa* L. cv. 'Ambassador') was analyzed under controlled conditions simulating the winter glasshouse atmosphere. Prior to measurements the plants were grown in CO₂-enriched air of 1000 $\mu\text{mol} \cdot \text{mol}^{-1}$, at a photosynthetic photon flux density (PPFD) of 280 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (400-700 nm) and a day/night air temperature of 16/13 degrees C. Short-term changes in CO₂ concentration significantly changed the initial gradient of the photosynthetic response to incident PPFD. Maximum photosynthetic efficiency of the crop increased from 0.041 $\text{mol} \cdot \text{CO}_2 \cdot \text{mol} \cdot \text{photons}^{-1}$ (equivalent to 8.2 $\mu\text{g} \cdot \text{CO}_2 \cdot \text{J}^{-1}$) and 9.4% on an energy basis) at 350 $\mu\text{mol} \cdot \text{mol}^{-1}$ to 0.055 $\text{mol} \cdot \text{CO}_2 \cdot \text{photons}^{-1}$ (10.9 $\mu\text{g} \cdot \text{CO}_2 \cdot \text{J}^{-1}$) and 12.7% on an energy basis) at 1000 $\mu\text{mol} \cdot \text{mol}^{-1}$. Transfer from low to high CO₂ also lowered the light compensation point, but did not affect dark respiration. The large response of P_n to transient changes in CO₂ indicated that the lettuce canopy did not acclimate to growth in

1000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, in contrast with the effect of growth in high CO_2 on P-n in single mature leaves reported earlier. A reduction in air temperature from 16 to 6 degrees C at a concentration of 1000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ halved the rate of dark respiration and reduced the light compensation point, but had no direct effect on the maximum efficiency with which the crop utilized light. Subsequently, at low light (below 200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) P-n was greater at 6 than 16 degrees C. Between a PPFD of 250 and 300 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ canopy P-n was similar at all temperatures. Addition of 2.0 $\mu\text{mol mol}^{-1}$ nitric oxide to an atmosphere of 1000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ caused a rapid and reversible reduction of canopy P-n which was greater at the lowest temperatures. The average inhibition was 6.6% at 16 degrees C and 28.8% at 6 degrees C; this was not explained by differences in the rate of pollutant uptake, which was less in the cooler conditions. The results are discussed in relation to development of optimal growing conditions for production of glasshouse lettuce at low light and low temperature during winter in the UK.

KEYWORDS: CONTROLLED-ENVIRONMENT CHAMBER, DIOXIDE, ENRICHMENT, GROWTH, INHIBITION, INTEGRATED ANALYSIS, LEAF PHOTOSYNTHESIS, LIGHT INTERCEPTION, PLANTS, WINTER LETTUCE

320

Caporn, S.J.M., T.A. Mansfield, and D.W. Hand. 1991. Low temperature-enhanced inhibition of photosynthesis by oxides of nitrogen in lettuce (*Lactuca sativa* L). *New Phytologist* 118(2):309-313.

The response of photosynthetic gas exchange to oxides of nitrogen ($\text{NO}(x)$) was studied in leaves of lettuce (*Lactuca sativa* L.) at different temperatures. Exposure to high concentrations (e.g. 1.3- $\mu\text{mol NO}(x) \text{ mol}^{-1}$), similar to those often found in commercial glasshouses, caused a rapid inhibition of the net assimilation of CO_2 . This appeared to be by a direct effect on photosynthesis rather than by a change in the stomatal conductance. In ambient CO_2 (345- $\mu\text{mol mol}^{-1}$), the percentage inhibition at 10 and 5-degrees-C was approximately 3 x and 5 x, respectively, that measured at 20- degrees-C. This effect of temperature also occurred when measured in CO_2 enriched air (1050- $\mu\text{mol mol}^{-1}$), which would normally accompany $\text{NO}(x)$ in a glasshouse. The extent of photosynthetic inhibition caused by $\text{NO}(x)$ was, however, always less in high than in low CO_2 . The results suggest that when burning fuel to raise the CO_2 concentration and heat the glasshouse air, growers should avoid generating high concentrations of $\text{NO}(x)$ in conditions of low temperature.

KEYWORDS: CO_2 - ENRICHMENT, GROWTH, NO_2 , PLANTS, SO_2 , SULFUR-DIOXIDE, TOMATO

321

Cardon, Z.G. 1996. Influence of rhizodeposition under elevated CO_2 on plant nutrition and soil organic matter. *Plant and Soil* 187(2):277-288.

Atmospheric CO_2 concentrations can influence ecosystem carbon storage through net primary production (NPP), soil carbon storage, or both. In assessing the potential for carbon storage in terrestrial ecosystems under elevated CO_2 , both NPP and processing of soil organic matter (SOM), as well as the multiple links between them, must be examined. Within this context, both the quantity and quality of carbon flux from roots to soil are important, since roots produce specialized compounds that enhance nutrient acquisition (affecting NPP), and since the flux of organic compounds from roots to soil fuels soil microbial activity (affecting processing of SOM). From the perspective of root physiology, a technique is described which uses genetically engineered bacteria to detect the distribution and amount of flux of particular compounds from single roots to non-sterile soils. Other

experiments from several labs are noted which explore effects of elevated CO_2 on root acid phosphatase, phosphomonoesterase, and citrate production, all associated with phosphorus nutrition. From a soil perspective, effects of elevated CO_2 on the processing of SOM developed under a C4 grassland but planted with C3 California grassland species were examined under low (unamended) and high (amended with 20 g m^{-2} NPK) nutrients; measurements of soil atmosphere $\delta^{13}\text{C}$ combined with soil respiration rates show that during vegetative growth in February, elevated CO_2 decreased respiration of carbon from C4 SOM in high nutrient soils but not in unamended soils. This emphasis on the impacts of carbon loss from roots on both NPP and SOM processing will be essential to understanding terrestrial ecosystem carbon storage under changing atmospheric CO_2 concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION, ECOSYSTEMS, ENRICHMENT, GROWTH, NITROGEN, RESPONSES, RHIZOSPHERE, ROOTS, TALLGRASS PRAIRIE

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Cardon, Z.G., J.A. Berry, and I.E. Woodrow. 1995. Fluctuating $[\text{CO}_2]$ drives species-specific changes in water use efficiency. *Journal of Biogeography* 22(2-3):203-208.

We have investigated the effects of fluctuating carbon dioxide (CO_2) concentration on water use efficiency of *Zea mays* L. and *Phaseolus vulgaris* L. We found that species-specific kinetics of stomatal movements combine with photosynthetic characteristics to influence shea-term water use efficiency strongly under fluctuating environmental conditions. Specifically, under oscillating $[\text{CO}_2]$, average transpiration in *Z. mays* was driven higher than that observed at steady-state at the median CO_2 concentration, while average photosynthesis remained fairly constant. Consequently, water use efficiency was lower during the fluctuations in $[\text{CO}_2]$ than it was at the steady, median $[\text{CO}_2]$. Under similar oscillations in $[\text{CO}_2]$, stomatal conductance and transpiration of *P. vulgaris* were driven lower than observed at steady-state at the median $[\text{CO}_2]$. A concomitant slight restriction of photosynthesis balanced this decrease in transpiration, and in this case water use efficiency under fluctuating $[\text{CO}_2]$ remained practically constant in *P. vulgaris*. The frequency of oscillations in $[\text{CO}_2]$ interacted with asymmetries in stomatal opening and closing kinetics in both *Z. mays* and *P. vulgaris* to determine the extent to which average transpiration (and water use efficiency in *Z. mays*) departed during fluctuations from the steady-state condition at the median CO_2 level.

KEYWORDS: LIGHT, RESPONSES

323

Cardon, Z.G., and R.B. Jackson. 1995. Root acid-phosphatase-activity in bromus-hordeaceus and avena- barbata remains unchanged under elevated $[\text{CO}_2]$. *Plant Physiology* 108(2):148.

324

Carey, E.V., R.M. Callaway, and E.H. DeLucia. 1997. Stem respiration of ponderosa pines grown in contrasting climates: Implications for global climate change. *Oecologia* 111(1):19-25.

We examined the effects of climate and allocation patterns on stem respiration in ponderosa pine (*Pinus ponderosa*) growing on identical substrate in the cool, moist Sierra Nevada mountains and the warm, dry, Great Basin Desert. These environments are representative of current climatic conditions and those predicted to accompany a doubling of atmospheric CO_2 , respectively, throughout the range of many western

north American conifers. A previous study found that trees growing in the desert allocate proportionally more biomass to sapwood and less to leaf area than montane trees. We tested the hypothesis that respiration rates of sapwood are lower in desert trees than in montane trees due to reduced stem maintenance respiration (physiological acclimation) or reduced construction cost of stem tissue (structural acclimation). Maintenance respiration per unit sapwood Volume at 15 degrees C did not differ between populations (desert: 6.39 +/- 1.14 SE mu mol m(-3) s(-1), montane: 6.54 +/- 1.13 SE mu mol m(-3) s(-1), P = 0.71) and declined with increasing stem diameter (P = 0.001). The temperature coefficient of respiration (Q(10)) varied seasonally within both environments (P = 0.05). Construction cost of stem sapwood was the same in both environments (desert: 1.46 +/- 0.009 SE g glucose g(-1) sapwood, montane: 1.48 +/- 0.009 SE glucose g(-1) sapwood, P = 0.14). Annual construction respiration calculated from construction cost, percent carbon and relative growth rate was greater in montane populations due to higher growth rates. These data provide no evidence of respiratory acclimation by desert trees. Estimated yearly stem maintenance respiration was greater in large desert trees than in large montane trees because of higher temperatures in the desert and because of increased allocation of biomass to sapwood. By analogy, these data suggest that under predicted increases in temperature and aridity, potential increases in aboveground carbon gain due to enhanced photosynthetic rates may be partially offset by increases in maintenance respiration in large trees growing in CO2-enriched atmospheres.

KEYWORDS: ABOVEGROUND PARTS, ACCLIMATION, ALLOCATION, CARBON, CO2, HINOKI FOREST TREE, MAINTENANCE RESPIRATION, PINUS-TAEDA, SCOTS PINE, TEMPERATURE

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Carey, E.V., E.H. DeLucia, and J.T. Ball. 1996. Stem maintenance and construction respiration in *Pinus ponderosa* grown in different concentrations of atmospheric CO2. *Tree Physiology* 16(1-2):125-130.

To determine whether long-term growth in enriched CO2 atmospheres changes the woody tissue respiration component of aboveground carbon budgets, we measured woody tissue respiration of stems of 3-year-old *ponderosa* pine (*Pinus ponderosa* Laws.) grown in ambient (350 ppm) or twice ambient (700 ppm) atmospheric CO2 concentrations in open-top field chambers located in Placerville, CA. Total respiration rate was measured by gas exchange, and construction respiration was calculated from the construction cost, percent carbon of stem samples and relative growth rate. Maintenance respiration was determined as the difference between total and construction respiration. The Q(10) of respiration was greater in stems grown in elevated CO2 than in stems grown in ambient CO2 (2.20 versus 1.67). As a result, mean daily respiration per unit volume of wood modeled for the month of September was greater in trees growing in elevated CO2 than in ambient CO2 (46.75 versus 40.45 mol m(-3) day(-1)). These effects of atmospheric CO2 concentration were not the result of differences in relative growth rate. Calorimetric analyses of woody tissue construction cost indicated no difference between treatments; however, trees in the elevated CO2 treatment showed a 1% lower carbon concentration than trees in the ambient CO2 treatment. Estimates of construction respiration did not differ between treatments, confirming that the treatment differences in mean daily respiration rate were attributable to the maintenance component. Under future predicted atmospheric conditions, changes in the maintenance respiration of woody tissue may lead to an increase in the respiration component of whole-plant carbon budgets of *ponderosa* pine. Our results suggest that potential increases in the maintenance component of stem respiration should be considered when modeling the response of forest stand growth to enriched CO2 atmospheres.

KEYWORDS: COST, ELEVATED CARBON-DIOXIDE, ENRICHMENT, FIELD, FOREST TREE, LEAVES, PLANT RESPIRATION,

SEEDLINGS, TEMPERATURE

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Carlsson, A.S., G. Wallin, and A.S. Sandelius. 1996. Species- and age-dependent sensitivity to ozone in young plants of pea, wheat and spinach: Effects on acyl lipid and pigment content and metabolism. *Physiologia Plantarum* 98(2):271-280.

Acyl lipids and pigments were analyzed in young plants of garden pea, spring wheat and spinach exposed to <5 or 65 nl l(-1) ozone 12 h per day for 6 days. In one set of experiments, the plants were exposed to (CO2)-C-14 for 2 h 3 days prior to ozone exposure. The plants responded differently to the moderately enhanced level of ozone used. Spinach was not at all sensitive while in both pea and wheat, leaves of different ages differed in ozone sensitivity. In pea, ozone sensitivity increased with leaf age. In the second and third oldest leaves, the amounts of galactolipids per leaf area and the proportions of 18:3 of the total lipid extract and of phosphatidylglycerol decreased. In the second oldest leaf, ozone also caused a decreased proportion of 18:3 of monogalactosyldiacylglycerol. In the fourth oldest leaf, Lipid composition and galactolipid unsaturation was unaffected, but ozone caused decreased leaf expansion resulting in increased acyl lipid content per leaf area. In both the first and second leaves of wheat, ozone fumigation caused a marked decrease in the content of monogalactosyldiacylglycerol and in the first leaf, the contents of phosphatidylcholine and phosphatidylethanolamine increased. The proportion of 18:3 in phosphatidylcholine was larger in ozone-fumigated than in control plants, while the reverse applied for phosphatidylglycerol. In the oldest sampled leaves of pea and wheat, ozone caused an increase in the radioactivity associated with beta-carotene, indicating increased turnover. Thus, while spinach was unaffected, in both pea and wheat ozone caused a decrease in the proportion of chloroplast membrane lipids to non-chloroplast membrane lipids in older leaves while younger leaves were less sensitive.

KEYWORDS: LEAVES, MODERATELY ENHANCED LEVELS, PISUM-SATIVUM, POLAR LIPIDS, PROTECTION, TRITICUM-AESTIVUM

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Carlsson, B.A., and T.V. Callaghan. 1994. Impact of climate-change factors on the clonal sedge *Carer bigelowii* - implications for population-growth and vegetative spread. *Ecography* 17(4):321-330.

Hypothesized life-cycle responses to climate change for the arctic, clonal perennial *Carer bigelowii* are constructed using a range of earlier observations and experiments together with new information from monitoring and an environmental perturbation study. These data suggest, that under current climate change scenarios, increases in CO2, temperature and nutrient availability would promote growth in a qualitatively similar way. The evidence suggests that both tiller size and daughter tiller production will increase, and be shifted towards production of phalanx tillers which have a greater propensity for flowering. Furthermore, age at tillering as well as tiller life span may decrease, whereas survival of younger age classes might be higher. Mathematical models using experimental data incorporating these hypotheses were used to a) integrate the various responses and to calculate the order of magnitude of changes in population growth rate (lambda), and b) to explore the implications of responses in individual demographic parameters for population growth rate. The models suggest that population growth rate following climate change might increase significantly, but not unrealistically so, with the younger, larger, guerilla tillers being the most important tiller categories contributing to lambda. The rate of vegetative spread is calculated to more than double, while cyclical trends in flowering and population growth are predicted to decrease substantially.

KEYWORDS: CARBON DIOXIDE, DWARF-SHRUB, DYNAMICS, ELEVATED CO₂, ENVIRONMENTAL-CHANGE, ERIOPHORUM VAGINATUM, PLANTS, RESPONSES, SIZE, TUSsock TUNDRA

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Carmi, A. 1993. Effects of shading and CO₂ enrichment on photosynthesis and yield of winter grown tomatoes in subtropical regions. *Photosynthetica* 28(3):455-463.

The effects of exposing winter-grown tomato (*Lycopersicon esculentum* L.) to various sunlight irradiances and CO₂ concentrations, on dark respiration (R(D)), night respiration (R(N)), net photosynthetic-rate (P(N)), dry matter production (DMP), yield earliness and yield amount were studied. Plants were grown in greenhouses under controlled temperatures and exposed to: full (FS) or half (HS) sunlight irradiance in combination with atmospheric (A) or enriched (E) concentrations of 300-330 or 1400-1500 g(CO₂) m⁻³, respectively. The P(N) of intact leaves at noontime reached 10.7, 15.2, 5.9 and 9.6 μmol(CO₂) m⁻² s⁻¹ in treatments of FSA, FSE, HSA and HSE, respectively. The irradiances on the upper leaf surface during the P(N) measurements ranged between 160-190 and 450-550 μmol m⁻² s⁻¹ in the HS and FS treatments, respectively. R(D) of leaves which were kept in darkness following the P(N) measurement arrived at efflux of 2.6, 2.5, 1.4 and 1.4 μmol(CO₂) m⁻² s⁻¹ while their R(N) (between 20:00 and 24:00) reached values of 0.9, 1.3, 0.8 and 0.8 μmol(CO₂) m⁻² s⁻¹ in treatments of FSA, FSE, HSA and HSE, respectively. Elevating the CO₂ concentration from 300 to 1500 g m⁻³ increased P(N) by 16, 28, 30 and 46% under an irradiance of 160 μmol m⁻² s⁻¹, and 19, 34, 59 and 44% under irradiance of 320 μmol m⁻² s⁻¹ in the FSA, FSE, HSA and HSE treatments, respectively. Increasing the measurement irradiance from 160 to 320 μmol m⁻² s⁻¹ enhanced P(N) by 69, 78, 23 and 49% in an atmosphere of 300 g m⁻³ CO₂, and by 73, 84, 49 and 47% in an atmosphere of 1500 g m⁻³ CO₂, in the FSA, FSE, HSA and HSE treatments, respectively. DMP was strongly influenced by the different environmental conditions and the total dry matter accumulation in the shoot per plant during 145 d reached 580, 347, 398 and 235 g in the FSA, FSE, HSA and HSE treatments, respectively. CO₂ enrichment promoted early yield under both full and partial sunlight irradiance. The HSE treatment led to earlier yield harvesting than the FSA and HSA treatments. The yield of the seven first trusses reached 6.8, 4.6, 5.7 and 3.2 kg per plant in the FSA, FSE, HSA and HSE treatments, respectively. Some increase in fruit fresh matter and diameter of fruits was detected in the CO₂-enriched treatments as compared to the non-enriched ones. Thus the combination of moderate shading and CO₂ enrichment might provide a more productive option for winter-grown tomatoes in regions of subtropical climate, even in the winter, than the conventional management of aerated greenhouses without CO₂ enrichment which are exposed to full sunlight.

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Carpenter, S.R., S.G. Fisher, N.B. Grimm, and J.F. Kitchell. 1992. Global change and fresh-water ecosystems. *Annual Review of Ecology and Systematics* 23:119-139.

KEYWORDS: AQUATIC SYSTEMS, CADDISFLY POPULATION, CO₂-INDUCED CLIMATIC-CHANGE, DESERT STREAM, GRADIENT HEADWATER STREAMS, GREAT- LAKES BASIN, ORGANIC-CARBON, POTENTIAL CHANGES, THERMAL HABITAT, WATER-RESOURCES

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Carter, E.B., M.K. Theodorou, and P. Morris. 1997. Responses of *Lotus corniculatus* to environmental change .1. Effects of elevated CO₂, temperature and drought on growth and plant development. *New*

Phytologist 136(2):245-253.

Five clonal plants of three genotypes of *Lotus corniculatus* were grown in each of eight controlled environments under combinations of two temperature regimes (18/10 degrees C and 25/15 degrees C), two CO₂ concentrations (ambient and 700 ppmv) and two water applications (ad libitum or 60% droughted). Plants were harvested at full flower and measurements made of plant growth and development. Of the three environmental variables studied, higher growth temperatures resulted in the largest number of significant changes to the measured variables. Reproductive capacity, growth rate, shoot biomass, water use efficiency and chlorophyll content were all enhanced by raising the growth temperature from 18 to 25 degrees C. Doubling the CO₂ concentration enhanced the growth rate, shoot biomass and water use efficiency and ameliorated some of the effects of drought, including reproductive capacity, and biomass production, but reduced flowering time, specific leaf area, and chlorophyll content of both droughted and undroughted plants. Drought alone reduced reproductive capacity, growth rate and above ground biomass but significantly increased root biomass in all environments. The agronomic effects resulting from a combined increase in growth temperature, doubled CO₂ concentration and mild drought in this experiment were a shorter vegetative period and an increase in biomass, but a fall in reproductive capacity.

KEYWORDS: CARBON DIOXIDE, EFFICIENCY, ENRICHMENT, INCREASING CO₂, N₂ FIXATION, PHOTOSYNTHESIS, RESPIRATION, WATER-STRESS, WHITE CLOVER, YIELD

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Carter, E.B., M.K. Theodorou, and P. Morris. 1999. Responses of *Lotus corniculatus* to environmental change. 2. Effect of elevated CO₂, temperature and drought on tissue digestion in relation to condensed tannin and carbohydrate accumulation. *Journal of the Science of Food and Agriculture* 79(11):1431-1440.

Clonal plants of three genotypes of *Lotus corniculatus* (cv Lee) were grown in eight controlled environments under combinations of two temperature regimes, two CO₂ concentrations and two watering regimes. Condensed tannins (proanthocyanidins), in-vitro digestibility, initial rates of gas evolution as an indicator of the initial rates of fermentation of the substrate), volatile fatty acid evolution, and non-structural carbohydrate (NSC) levels were determined in leaves, stems and roots at full flowering. Under control conditions (average midsummer conditions in the United Kingdom) the total condensed tannin content of leaves varied six-fold between genotypes but condensed tannin contents in stems and roots were similar. Condensed tannin levels were significantly increased in leaves and stems of all three genotypes by doubling the CO₂ concentration while raising the temperature towards the optimum for growth significantly reduced condensed tannin levels. Drought stress significantly reduced condensed tannin levels in leaves and, particularly, in roots. Nutritive value was inversely related to condensed tannin levels in leaves and a negative relationship was observed between condensed tannin concentrations of more than 25-30 g kg⁻¹ dry matter and the initial rates of gas evolution when subjected to in-vitro fermentation with rumen micro-organisms. In leaves, digestibility was significantly increased by drought and by increasing temperature but reduced by high CO₂. In stems, digestibility was significantly increased by drought, but not significantly affected by increasing temperature, or by high CO₂ alone. In roots, digestibility was significantly increased by drought, and decreased by increasing temperature or CO₂. Increasing the growth temperature towards optimum growth reduced the content of NSC in all tissues with the greatest changes occurring in root tissue. Doubling the CO₂ concentration increased NSC levels in leaves and stems with starch content more than doubled under high CO₂ while, in roots, increased levels were only observed in combination with drought stress. There was a linear correlation between condensed tannin concentration and total

NSC that was positive for leaves, neutral for stems and negative for roots. The relationship between carbohydrate levels and rates of gas production was negative for leaves and positive for stem and roots. (C) 1999 Society of Chemical Industry.

KEYWORDS: DIGESTIBILITY, GAS-PRODUCTION, GROWTH, ISOSYNTHETIC STRAINS, METABOLISM, PEDUNCULATUS, PROANTHOCYANIDINS, PROTEIN, RUMEN, SHEEP

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Carter, G.A., J. Rebbeck, and K.E. Percy. 1995. Leaf optical-properties in liriiodendron-tulipifera and pinus- strobus as influenced by increased atmospheric ozone and carbon-dioxide. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 25(3):407-412.

Seedlings of Liriiodendron tulipifera L. and Pinus strobus L. were grown in open-top chambers in the field to determine leaf optical responses to increased ozone (O-3) or O-3 and carbon dioxide (CO2). In both species, seedlings were exposed to charcoal-filtered air, air with 1.3 times ambient O-3 concentrations (1.3X), or air with 1.3 times ambient O-3 and 700 $\mu\text{L} \cdot \text{L}^{-1}$ CO2 (1.3X + CO2). Exposure to 1.3X increased reflectance in the 633-697 nm range in L. tulipifera. Also, 1.3X decreased transmittance within the 400-420 nm range, increased transmittance at 686-691 nm, and decreased absorptance at 655-695 nm. With 700 $\mu\text{L} \cdot \text{L}^{-1}$ CO2, O-3 did not affect reflectance in L. tulipifera, but decreased transmittance and increased absorptance within the 400-421 nm range and increased transmittance and decreased absorptance in the 694-697 nm range. Under 1.3X, reflectance in P. strobus was not affected. However, 1.3X + CO2 increased pine reflectance in the 538-647, 650, and 691-716 nm ranges. Transmittances and absorptances were not determined for P. strobus. Reflectance in both species, and transmittance and absorptance in L. tulipifera, were most sensitive to O-3 near 695 nm. Reflectance at 695 nm, but particularly the ratio of reflectance at 695 nm to reflectance at 760 nm, was related closely to ozone-induced decreases in leaf chlorophyll contents, particularly chlorophyll a ($r(2) = 0.82$).

KEYWORDS: CHLOROPHYLL CONTENT, ELEVATED CO2, INJURY, LEAVES, NITROGEN, RED EDGE, RESPONSES, SLASH PINE, SPECTRAL REFLECTANCE

333

Case, A.L., P.S. Curtis, and A.A. Snow. 1998. Heritable variation in stomatal responses to elevated CO2 in wild radish, Raphanus raphanistrum (Brassicaceae). *American Journal of Botany* 85(2):253-258.

Rising atmospheric carbon dioxide may affect plant populations in the short term through effects on photosynthesis and carbon allocation, and over the long term as an agent of natural selection. To test for heritable effects of elevated CO2 on stomatal responses and plant fecundity in Raphanus raphanistrum, we grew plants from 12 paternal families in outdoor open-top chambers at ambient (35 Pa) or elevated (67 Pa) CO2. Contrary to results from a previous study of this species, total flower and fruit production were marginally lower under elevated CO2. Across families, stomatal index and guard cell length showed little response to CO2 enrichment, but these characters varied significantly among paternal families in both the direction and magnitude of their response to changing CO2. Although these family-by-CO2 interactions suggest that natural selection might affect stomatal characters when ambient CO2 levels increase, we found no significant correlation between either character and flower or fruit production. Therefore, our data suggest that while heritable variation for stomatal index and guard cell length exists in this population, selection due to increasing CO2 is not likely to act on these traits because they had no detectable effect on lifetime fecundity.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DENSITY, ENRICHMENT, EVOLUTION, GAS-EXCHANGE, GROWTH, LEAVES, PERFORMANCE, PLANTS

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Casella, E., and J.F. Soussana. 1997. Long-term effects of CO2 enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany* 48(311):1309-1321.

Perennial ryegrass swards were grown in large containers on a soil, at two N fertilizer supplies and were exposed during two years in highly ventilated plastic tunnels to elevated (700 $\mu\text{L} \cdot \text{L}^{-1}$ [CO2]) or ambient atmospheric CO2 concentration at outdoor temperature and to a 3 degrees C increase in air temperature in elevated CO2. The irrigation was adjusted to obtain a soil water deficit during summer. The daily net C assimilation was increased in elevated CO2 by 29 and 36% at the low and high N supplies, respectively. Canopies grown in elevated CO2 for 14 to 27 months photosynthesized significantly less rapidly, in both elevated and normal CO2 concentrations, than their counterparts developed in ambient CO2, but the magnitude of this effect was small (-8% to -13%). Elevated CO2 resulted in a large increase in the fructan concentration in the pseudostems and laminae (+46% and +189%, respectively). In elevated CO2, the hexose and sucrose pool increased by 28% in the laminae, whereas it did not vary significantly in the pseudostems. A 3 degrees C temperature increase in elevated CO2 did not affect significantly the average WSC concentrations in the pseudostems and laminae. The elevated CO2 effects on the net C assimilation and on the nocturnal shoot respiration were greater in summer than in spring. On average, a 35% increase in the below-ground respiration was measured in elevated CO2. At the high N supply, a 3 degrees C increase in air temperature led to a decline in the below-ground respiration due to a low soil moisture. The below-ground carbon storage was increased by 32% and 96% in elevated CO2 at the low and high N supplies, respectively, with no significant increased temperature effect. The role for the below-ground carbon storage of CO2-induced changes in the root fraction of the grass and of temperature-induced changes in the moisture content of the soil are discussed.

KEYWORDS: ACCLIMATION, ATMOSPHERE, DIOXIDE CONCENTRATION, ELEVATED CO2, GROWTH, LOLIUM-PERENNE, NET PHOTOSYNTHESIS, NITROGEN, PLANT-RESPONSES, SOIL CARBON

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Casella, E., J.F. Soussana, and P. Loiseau. 1996. Long-term effects of CO2 enrichment and temperature increase on a temperate grass sward .1. Productivity and water use. *Plant and Soil* 182(1):83-99.

Perennial ryegrass swards were grown in large containers on a soil, at two N fertilizer supplies, and were exposed over two years in highly ventilated plastic tunnels to elevated (700 $\mu\text{L} \cdot \text{L}^{-1}$ [CO2]) or ambient atmospheric CO2 concentration at outdoor temperature and to a 3 degrees C increase in air temperature in elevated CO2. These swards were either fully irrigated (kept at field capacity) in each climatic condition (W+), or received the same amount of water in the three climate treatments (W-). In the latter case, the irrigation was adjusted to obtain a soil water deficit during summer and drainage in winter. Using a lysimeter approach, the evapotranspiration, the soil water balance, the productivity (dry-matter yield) and the water use efficiency of the grass swards were measured. During both years, elevated CO2 increased the annual above-ground drymatter yield of the W-swards, by 19% at N- and by 14% at N+. Elevated CO2 modified yield to a variable extent during the growing season: a small, and sometime not significant effect (+6%, on average) was obtained in spring and in autumn, while the summer growth response was stronger (+48%, on average). In elevated CO2, the

temperature increase effect on the annual above-ground dry-matter yield was not significant, due to a gain in dry-matter yield in spring and in autumn which was compensated for by a lower summer productivity. Elevated CO₂ slightly reduced the evapotranspiration during the growing season and increased drainage by 9% during winter. A supplemental 3 degrees C in elevated CO₂ reduced the drainage by 29-34%, whereas the evapotranspiration was increased by 8 and 63% during the growing season and in winter, respectively. During the growing season, the soil moisture content at W- and at the high N supply declined gradually in the control climate, down to 20-30% of the water holding capacity at the last cut (September) before rewatering. This decline was partly alleviated under elevated CO₂ in 1993, but not in 1994, and was enhanced at +3 degrees C in elevated CO₂. The water use efficiency of the grass sward increased in elevated CO₂, on average, by 17 to 30% with no significant interaction with N supply or with the soil water deficit. The temperature increase effect on the annual mean of the water use efficiency was not significant. Highly significant multiple regression models show that elevated CO₂ effect on the dry-matter yield increased with air temperatures above 14.5 degrees C and was promoted by a larger soil moisture in elevated compared to ambient CO₂. The rate of change in relative dry-matter yield at +3 degrees C in elevated CO₂ became negative for air temperatures above 18.5 degrees C and was reduced by a lower soil moisture at the increased air temperature. Therefore, the altered climatic conditions acted both directly on the productivity and on the water use of the grass swards and, indirectly, through changes in the soil moisture content.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CROP YIELD, EFFICIENCY, ELEVATED CO₂, GROWTH, LEAF-AREA, LIMITED CONDITIONS, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PHOTOSYNTHESIS

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Cater, M., P. Simoncic, and F. Batic. 1999. Pre-dawn water potential and nutritional status of pedunculate oak (*Quercus robur* L.) in the north-east of Slovenia. *Phyton-Annales Rei Botanicae* 39(4):13-21.

In the 1997 growth period monthly measurements of pre-dawn water potential, electrical resistance of the cambial zone, groundwater level and quality together with annual dynamics of macronutrient elements in leaves and heavy metals (Zn, Pb, Cd) were performed. Two plots having different groundwater tables and crown defoliation were studied in the pedunculate oak forest complex (*Quercus Roboris-Carpinetum* M. Wraber) in the north-east of Slovenia. Results showed lower (more negative) values of pre-dawn water potential and higher values of cambial electrical resistance on the plot with greater crown defoliation, which also had a lower groundwater table. Groundwater seems to be the key factor in the process of oak decline.

KEYWORDS: DECLINE, DROUGHT, ELEVATED CO₂, EMBOLISM, FIR, GROWTH, PHOTOSYNTHESIS, SEEDLINGS, STANDS, STRESS

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Catovsky, S., and F.A. Bazzaz. 1999. Elevated CO₂ influences the responses of two birch species to soil moisture: implications for forest community structure. *Global Change Biology* 5(5):507-518.

Increased levels of atmospheric CO₂ may alter the structure and composition of plant communities by affecting how species respond to their physical and biological environment. We investigated how elevated CO₂ influenced the response of paper birch (*Betula papyrifera* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) seedlings to variation in soil moisture. Seedlings were grown for four months on a soil moisture gradient, individually and in mixed species stands, in controlled environment facilities at ambient (375 μ L L⁻¹) and elevated (700 μ L L⁻¹) atmospheric CO₂. For both individually and competitively grown

paper birch seedlings, there was a greater CO₂ growth enhancement for seedlings watered less frequently than for well-watered seedlings. This differential change in CO₂ responsiveness across the moisture gradient reduced the difference in seedling growth between high and low water levels and effectively broadened the regeneration niche of paper birch. In contrast, for yellow birch seedlings, elevated CO₂ only produced a significant growth enhancement at the wet end of the soil moisture gradient, and increased the size difference between seedlings at the two ends of the gradient. Gas exchange measurements showed that paper birch seedlings were more sensitive than yellow birch seedlings to declines in soil moisture, and that elevated CO₂ reduced this sensitivity. Additionally, elevated CO₂ improved survival of yellow birch seedlings growing in competition with paper birch in dry stands. Thus, elevated CO₂ may influence regeneration patterns of paper birch and yellow birch on sites of differing soil moisture. In the future, as atmospheric CO₂ levels rise, growth of paper birch seedlings and survival of yellow birch seedlings may be enhanced on xeric sites, while yellow birch may show improved growth on mesic sites.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CONTRASTING SHADE TOLERANCE, COOCCURRING BIRCH, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE, PINUS-TAEDA SEEDLINGS, TERRESTRIAL ECOSYSTEMS, WATER-STRESS

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Catsky, J., J. Pospisilova, J. Solarova, H. Synkova, and N. Wilhelmova. 1995. Limitations on photosynthesis under environment-simulating culture in-vitro. *Biologia Plantarum* 37(1):35-48.

Limitations on photosynthesis, characterized by leaf CO₂ exchange, chlorophyll fluorescence, and thylakoid structure, were studied under environmental conditions simulating culture in vitro. These were simulated by growing *Phaseolus vulgaris* plants in nutrient solution under high relative humidity of air (> 90%), and CO₂ concentrations (c(a)) that decreased with the development of photosynthetic activities during plant ontogeny (1200 to 300 mg m⁻³). The ontogeny of such model plants was more rapid, primary leaves reached photosynthetic maturity 2 to 3 d earlier and their life span was 7 to 14 d shorter than in control plants. Their photosynthetic activity in situ was limited, after reaching "photosynthetic maturity", similarly to plants grown in vitro. When measured under optimal conditions, however, 50 to 70% higher net photosynthetic rate (P(N)) were found in leaves of different ages as compared with plants grown under c(a) of 700 mg m⁻³ and a lower air humidity (30 - 35%). This increase in P(N) was associated with a high conductance for CO₂ transfer by adaxial and abaxial epidermes. In model plants, the dark respiration rate (R(D)) was almost twice that in the control, while the photorespiration rates were similar to controls; CO₂ compensation concentration was about 50% of that in controls. The ratios P(N)/R(D) were similar in control and in model plants. Chlorophyll a+b content in leaves of the model plants was lower than that in the control plants. Grana extent increased with plant age in the model plants while it decreased in the control ones. In both the stomal and granal membranes of the chloroplasts in model plants, a marked accumulation of carotenoids occurred independent of age. The ratio of variable to maximal fluorescence, F(v)/F(m), did not differ in the model and the control plants. In the control plants, photochemical quenching (qp) slightly increased with plant age and was not affected by CO₂ concentration present during measurement. In the model plants, qp increased with elevated CO₂ concentration in young plants and decreased in saturating CO₂ concentrations in older plants. Nonphotochemical quenching (q(NP)) was lower in the model plants and increased under CO₂ saturating conditions. Vitality index, Rfd, was markedly lower in the model plants than in the control ones and a decline was found in saturating CO₂ concentration.

Caulfield, F., and J.A. Bunce. 1994. Elevated atmospheric carbon-dioxide concentration affects interactions between spodoptera-exigua (lepidoptera, noctuidae) larvae and 2 host-plant species outdoors. *Environmental Entomology* 23(4):999-1005.

Beet armyworm, *Spodoptera exigua* (Hubner), larvae were placed on sugarbeet (*Beta vulgaris* L.) and pigweed (*Amaranthus hybridus* L.) plants in outdoor chambers in which the plants were growing at either the ambient (almost-equal-to 350 $\mu\text{mol liter}^{-1}$) or ambient plus 350 $\mu\text{mol liter}^{-1}$ (almost-equal-to 700 $\mu\text{mol liter}^{-1}$) carbon dioxide concentration. A series of experiments was performed to determine if larvae reduced plant growth differently at the two carbon dioxide concentrations in either species and if the insect growth or survival differed with carbon dioxide concentration. Leaf nitrogen, water, starch, and soluble carbohydrate contents were measured to assess carbon dioxide concentration effects on leaf quality. Insect feeding significantly reduced plant growth in sugarbeet plants at 350 $\mu\text{mol liter}^{-1}$ but not at 700 $\mu\text{mol liter}^{-1}$ nor in pigweed at either carbon dioxide concentration. Larval survival was greater on sugarbeet plants at the elevated carbon dioxide concentration. Increased survival occurred only if the insects were at the elevated carbon dioxide concentration and consumed leaf material grown at the elevated concentration. Leaf quality was only marginally affected by growth at elevated carbon dioxide concentration in these experiments. The results indicate that in designing experiments to predict effects of elevated atmospheric carbon dioxide concentrations on plant-insect interactions, both plants and insects should be exposed to the experimental carbon dioxide concentrations, as well as to as realistic environmental conditions as possible.

KEYWORDS: COTTON, ENRICHED CO₂ ATMOSPHERES, GROWTH, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LEAVES, PERIODS, PHOTOSYNTHESIS, RESPONSES, STARCH

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Cavender-Bares, J.M., P.B. Voss, and F.A. Bazzaz. 1998. Consequences of incongruency in diurnally varying resources for seedlings of *Rumex crispus* (Polygonaceae). *American Journal of Botany* 85(9):1216-1223.

The incongruency of diurnally varying resources essential to plants may detrimentally affect plants early in their development as indicated by reduced water use efficiency and carbon gain. Typical diurnal patterns of light and CO₂ availability in a mid-sized temperate herbaceous or forest gap were simulated in specially designed growth chambers. A sinusoidally varying CO₂ treatment (400 ppm minimum, 800 ppm maximum) approximated the diurnal cycle of CO₂ at the soil surface, while a steady-state CO₂ treatment (600 ppm) with the same average CO₂ concentration provided a control. Crossed with these two CO₂ treatments were two light regimes, one with 3 h of high light (850 $\mu\text{mol m}^{-2}\text{s}^{-1}$) in the morning (west side of a gap), and the other with 3 h of high light in the afternoon (east side). All treatments received baseline low light (55 $\mu\text{mol m}^{-2}\text{s}^{-1}$) for 14 h during the day. *Rumex crispus* was selected as a model species because of its rosette leaves, which grow close to the ground where diurnal CO₂ variation is greatest. The relative timing of diurnal variations in light and CO₂ significantly affected seedling water use efficiency, carbon gain, and morphology. Total biomass, photosynthetic rates, daily integrated carbon, water use efficiency, and leaf area were enhanced by morning exposure to high light. Seedlings that were exposed to peak values of light and CO₂ incongruently, i.e., those plants receiving intense afternoon light with diurnally varying CO₂, were detrimentally affected relative to control plants receiving intense afternoon light with steady-state CO₂. The results of this experiment indicate that the incongruent availability of required resources-such as light and CO₂-can detrimentally affect performance relative to when resources are

congruent. These contrasting resource regimes can occur on the east and west side of gaps.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, ELEVATED CO₂, FOREST, GAS-EXCHANGE, GROWTH, LIGHT, PLANTS, RESPONSES, WATER RELATIONS

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Cebrian, J. 1999. Patterns in the fate of production in plant communities. *The American Naturalist* 154(4):449-468.

I examine, through an extensive compilation of published reports, the nature and variability of carbon flow (i.e., primary production, herbivory, detrital production, decomposition, export, and biomass and detrital storage) in a range of aquatic and terrestrial plant communities. Communities composed of more nutritional plants (i.e., higher nutrient concentrations) lose higher percentages of production to herbivores, channel lower percentages as detritus, experience faster decomposition rates, and, as a result, store smaller carbon pools. These results suggest plant palatability as a main limiting factor of consumer metabolic and feeding rates across communities. Hence, across communities, plant nutritional quality may be regarded as a descriptor of the importance of herbivore control on plant biomass ("top-down" control), the rapidity of nutrient and energy recycling, and the magnitude of carbon storage. These results contribute to an understanding of how much and why the trophic routes of carbon flow, and their ecological implications, vary across plant communities. They also offer a basis to predict the effects of widespread enhancement of plant nutritional quality due to large-scale anthropogenic eutrophication on carbon balances in ecosystems.

KEYWORDS: CARBON BALANCE, ECOSYSTEMS, ELEVATED CO₂, FRESH-WATER, GROWTH RATE, HERBIVORY, MARINE WATERS, NITROGEN, NUTRIENT LIMITATION, ORGANIC-MATTER

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Centritto, M., and P.G. Jarvis. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). II. Photosynthetic capacity and nitrogen use efficiency. *Tree Physiology* 19(12):807-814.

Four clones of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) from two provenances, at 53.2 degrees N (Skidegate a and Skidegate b) and at 41.3 degrees N (North Bend a and North Bend b), were grown for three growing seasons in ambient (similar to 350 $\mu\text{mol mol}^{-1}$) and elevated (similar to 700 $\mu\text{mol mol}^{-1}$) CO₂ concentrations. The clones were grown in stress-free conditions (adequate nutrition and water) to assess the effect of elevated [CO₂] on tree physiology. Growth in elevated [CO₂] significantly increased instantaneous photosynthetic rates of the clonal Sitka spruce saplings by about 62%. Downward acclimation of photosynthesis (A) was found in all four clones grown in elevated [CO₂]. Rubisco activity and total chlorophyll concentration were also significantly reduced in elevated [CO₂]. Provenance did not influence photosynthetic capacity. Best-fit estimates of J(max) (maximum rate of electron transport), V-cmax (RuBP-saturated rate of Rubisco) and A(max) (maximum rate of assimilation) were derived from responses of A to intercellular [CO₂] by using the model of Farquhar et al. (1980). At any leaf N concentration, the photosynthetic parameters were reduced by growth in elevated [CO₂]. However, the ratio between J(max) and V-cmax was unaffected by CO₂ growth concentration, indicating a tight coordination in the allocation of N between thylakoid and soluble proteins. In elevated [CO₂] the more southerly clones had a higher initial N use efficiency (more carbon assimilated per unit of leaf N) than the more northerly clones, so that they had more N available for those processes or organs that were most limiting to growth at a particular time. This may explain the initial higher growth stimulation by elevated [CO₂] in the North Bend clones

than in the Skidegate clones.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO₂, GAS-EXCHANGE, GENE-EXPRESSION, LOBLOLLY-PINE TREES, NUTRITION, PLANTS, SEEDLINGS, TEMPERATURE

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Centritto, M., H.S.J. Lee, and P.G. Jarvis. 1999. Increased growth in elevated [CO₂]: an early, short-term response? *Global Change Biology* 5(6):623-633.

Saplings of four clones of Sitka spruce and cherry were grown for three and two growing seasons, respectively, in open top chambers at two CO₂ concentrations (approximate to 350 and approximate to 700 $\mu\text{mol mol}^{-1}$) to determine whether the increase in total biomass brought about by enhanced [CO₂] is a result of a transient or persistent effect in nonlimiting conditions. Classical growth analysis was applied to both species and mean current relative growth rate of total dry mass (R-T) and leaf dry mass (R-L), and period relative growth rate of total dry mass (R-T(t)) and leaf dry mass (R-L(t)) were calculated. Sitka spruce saplings and cherry seedlings showed a positive growth response to elevated [CO₂], and at the end of the experiments both species were approximate to 40% larger in elevated [CO₂] than in ambient [CO₂]. As a result, the period mean R-T(t) and R-L(t) were significantly higher in elevated [CO₂]. The differences in plant dry mass at the end of the experiments were a consequence of the more rapid growth in the early phase of exposure to elevated [CO₂]. After this initial phase mean R-T and R-L were similar or even lower in elevated [CO₂] than in ambient [CO₂]. NAR of both species was much higher in elevated [CO₂], whereas both LAR, SLA, and LMR showed the opposite trend. The higher LAR and SLA of plants in ambient [CO₂] contributed to a compensation by which they maintained R-T similar to that of elevated [CO₂] saplings despite lower NAR and photosynthetic rate. However, when the same size the trees were similar amongst the [CO₂] treatments, indicating that one of the main effects of elevated [CO₂] on tree growth is to speed-up early development in all aspects.

KEYWORDS: ACCLIMATION, AMBIENT, ATMOSPHERIC CO₂, BETULA-PENDULA ROTH, BIOMASS ALLOCATION, CARBON, PHOTOSYNTHESIS, PLANTAGO-MAJOR, PONDEROSA PINE, RESPIRATION

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Centritto, M., H.S.J. Lee, and P.G. Jarvis. 1999. Interactive effects of elevated [CO₂] and drought on cherry (*Prunus avium*) seedlings - I. Growth, whole-plant water use efficiency and water loss. *New Phytologist* 141(1):129-140.

Seeds of cherry (*Prunus avium*) were germinated and grown for two growing seasons in ambient (similar to 350 $\mu\text{mol mol}^{-1}$) or elevated (ambient + similar to 350 $\mu\text{mol mol}^{-1}$) CO₂ mole fractions in six open-top chambers. The seedlings were fertilized once a week, following Ingstad principles in order to supply mineral nutrients at free-access rates. In the first growing season gradual drought was imposed on rapidly growing cherry seedlings by withholding water for a 6-wk drying cycle. In the second growing season, the rapid onset of drought was imposed at the height of the growing season on the seedlings which had already experienced drought in the first growing season. Elevated [CO₂] significantly increased total dry-mass production in both water regimes, but did not ameliorate the growth response to drought of the cherry seedlings subjected to two sequential drying cycles. Water loss did not differ in either well watered or droughted seedlings between elevated and ambient [CO₂]; consequently whole-plant water-use efficiency (the ratio of total dry mass produced to total water consumption) was significantly increased. Similar patterns of carbon allocation between shoot and root were found in elevated and ambient [CO₂] when the seedlings were the

same size. Thus, elevated [CO₂] did not improve drought tolerance, but it accelerated ontogenetic development irrespective of water status.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DRY-WEIGHT, ENRICHMENT, GAS-EXCHANGE, LEAF-AREA, NUTRIENT AVAILABILITY, RESPONSES, SITCHENSIS BONG CARR, STRESS, WHEAT

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Centritto, M., H.S.J. Lee, and P.G. Jarvis. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). I. Plant growth, allocation and ontogeny. *Tree Physiology* 19(12):799-806.

Four clones of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) from two provenances, at 53.2 degrees N (Skidegate a and Skidegate b) and at 41.3 degrees N (North Bend a and North Bend b), were grown near Edinburgh (55.5 degrees N), U.K., for three growing seasons in ambient (similar to 350 $\mu\text{mol mol}^{-1}$) and elevated (similar to 700 $\mu\text{mol mol}^{-1}$) CO₂ concentrations under conditions of non-limiting water and nutrient supply. Bud phenology was not affected by elevated [CO₂] in the second growing season, but in the third year, the duration of shoot extension growth in three of the four clones (North Bend clones and Skidegate a) was significantly shortened, because of the suppression of lammas growth. Saplings in elevated [CO₂] had significantly greater dry masses of all components than saplings in ambient [CO₂]. However, comparison of relative component dry masses between plants of similar size showed no effect of [CO₂] treatment on plant allometric relationships. This finding, and the observed suppression of lammas growth by high [CO₂] during the third growing season suggests that the main effect of increasing [CO₂] is to accelerate sapling development. Clonal provenance did not affect dry mass production in ambient [CO₂]. However in elevated [CO₂] the more southerly clones significantly outperformed the more northerly clones when grown at a latitude close to the latitudinal provenance of the Skidegate clones. As atmospheric carbon dioxide concentration rises, such changes in the relative performance of genotypes may be exploited for economic gain through appropriate selection of provenances for forest plantings.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, BONG CARR, ENRICHMENT, FROST HARDINESS, INCREASE, NUTRITION, PHOTOSYNTHESIS, PHYSIOLOGY, SEEDLINGS

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Centritto, M., F. Magnani, H.S.J. Lee, and P.G. Jarvis. 1999. Interactive effects of elevated [CO₂] and drought on cherry (*Prunus avium*) seedlings - II. Photosynthetic capacity and water relations. *New Phytologist* 141(1):141-153.

Cherry seedlings (*Prunus avium*) were grown from seed for two growing seasons in three ambient [CO₂] (similar to 350 $\mu\text{mol mol}^{-1}$) and three elevated [CO₂] (ambient + similar to 350 $\mu\text{mol mol}^{-1}$) open-top chambers, and in three outside blocks. A drying cycle was imposed in both the growing seasons to half the seedlings: days 69-115 in the first growing season, and in the second growing season days 212-251 on the same seedlings which had already experienced drought. Stomatal conductance was significantly reduced in elevated [CO₂]-grown, unstressed seedlings in both the first and second growing seasons, but was not caused by a decrease in stomatal density. Droughted seedlings showed little or no reduction in stomatal conductance in response to elevated [CO₂]. However, stomatal conductance was highly correlated with soil water status. Photosynthetic rate increased significantly in response to elevated [CO₂] in both water regimes, leading to improvement in instantaneous transpiration efficiency over the whole duration of the experiment, but there was no relationship between instantaneous transpiration efficiency and long-term water use

efficiency. The A_{max} was strongly reduced in the second growing season, but unaffected by $[CO_2]$ treatment. Although photosynthetic rate was not down-regulated, Rubisco activity was decreased by elevated $[CO_2]$, possibly because of the increased leaf carbon:nitrogen ratio which had occurred by the ends of the two growing seasons. Elevated $[CO_2]$ did not improve plant water relations (for example, bulk leaf - water potential, osmotic potentials at full and zero turgor, relative water content at zero turgor, bulk modulus of elasticity of the cell) and thus did not increase water-stress tolerance of cherry seedlings.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO_2 , CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, STOMATAL CONTROL, TRANSPIRATION, TREES

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Ceulemans, R., I.A. Janssens, and M.E. Jach. 1999. Effects of CO_2 enrichment on trees and forests: Lessons to be learned in view of future ecosystem studies. *Annals of Botany* 84(5):577-590.

Because of their prominent role in global bioproductivity and because of their complex structure and function, forests and tree species deserve particular attention in studies on the likely impact of elevated atmospheric CO_2 on terrestrial vegetation. Besides a synoptic review of some of the most prominent above-ground response processes, particular attention is given to below-ground responses of trees to elevated atmospheric CO_2 , while some feedback processes and interactions with various biotic and abiotic factors are also briefly summarized. At the leaf level there is little evidence of the long-term loss of sensitivity to CO_2 that was suggested by earlier experiments with tree seedlings in pots. Future studies on photosynthesis measurements will probably not alter our conclusions about acclimation, but should focus more on respiration under elevated CO_2 , which is still poorly understood. At the tree level, the increase in growth observed in elevated CO_2 results from an increase in both leaf area and leaf photosynthetic rate (per unit leaf area). Tree growth enhancement is generally larger at high rates of nutrient supply; when nutrient supply rates do not meet growth rates, tree nutrient status declines and nutrients become limiting. In many studies at the canopy level, a shift in whole-tree carbon allocation pattern towards below-ground parts has been associated with increased atmospheric CO_2 concentrations. At the ecosystem level, a larger amount of carbon being allocated below-ground could show up by either (1) more root growth and turnover, (2) enhanced activity of root-associated microorganisms, (3) larger microbial biomass pools and enhanced microbial activity, or (4) increased losses of soil carbon through soil respiration. Fine root production is generally enhanced, but it is not clear whether this response would persist in a forest. As elevated CO_2 stimulates biomass production, litterfall and rhizodeposition also increase. This increased delivery of labile organic matter to the soil could influence soil microbial communities and subsequent decomposition rates, nutrient availability and carbon storage in soil. There are, however, contradictory hypotheses about the direction in which nutrient availability will be affected. Knowledge of the response of these and other ecophysiological processes to elevated CO_2 is the key to understanding the functioning of the whole forest ecosystem. Our current knowledge is sufficiently large with regard to how the carbon uptake process and individual tree growth respond under atmospheric changes, but more emphasis should be put in future experiments on the interactions between various processes, such as the carbon and nitrogen cycles, and on below-ground responses. (C) 1999 Annals of Botany Company.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED ATMOSPHERIC CO_2 , LEAF GAS- EXCHANGE, LONG-TERM CO_2 , MYCORRHIZAL COLONIZATION, OPEN-TOP CHAMBERS, PHOTOSYNTHETIC ACCLIMATION, PINE PINUS-PONDEROSA, SCOTS PINE, SOIL ORGANIC MATTER

348

Ceulemans, R., X.N. Jiang, and B.Y. Shao. 1995. Effects of elevated atmospheric CO_2 on growth, biomass production and nitrogen allocation of two Populus clones. *Journal of Biogeography* 22(2-3):261-268.

Two hybrid poplar (*Populus*) clones (i.e. fast growing clone Beaupre and slower growing clone Robusta) were grown from cuttings at close spacings in four open top chambers (OTCs) on the Campus of the University of Antwerpen, Belgium. The four OTCs represented two atmospheric CO_2 treatments, i.e. ambient and elevated (= ambient + 350 $\mu\text{mol mol}^{-1}$). Treatments lasted for a full growing season (April-November 1993) and results of the first growing season are being reported. In both clones the elevated CO_2 treatment resulted in a significant increase in plant height and in biomass production, both of stems and branches. Plants of both clones produced significantly more, but shorter, side branches under the elevated CO_2 treatment. In terms of biomass accumulation the slower growing clone Robusta benefited relatively more (+ 37%) from the elevated CO_2 concentrations than the fast growing clone Beaupre (+ 24%). In terms of leaf weight ratio, the slower growing clone became relatively more efficient under elevated CO_2 than the fast growing clone. The elevated atmospheric CO_2 treatment significantly increased the total leaf area per plant and leaf area index per OTC; maximum LAI increased by 18% in clone Beaupre and by only 8% in the slower growing clone Robusta. In the fast growing clone the increase in leaf area index was entirely caused by an increase in individual leaf area, while in the slower growing clone also a 5% higher leaf production was observed under the elevated CO_2 . The total length of the growing season was on average reduced by the elevated CO_2 treatment; in the slower growing clone mainly by an advancement of bud set and in the faster growing clone by a slight delay of bud break in early spring. In both clones elevated CO_2 decreased nitrogen concentration and increased C/N ratio in all plant organs, but no data for the below-ground compartment were available. Therefore, although similar trends in the responses to elevated atmospheric CO_2 were observed in both clones, the relative efficiency of these responses differed between the fast and the slower growing poplar clones, suggesting interactions between growth rate, growth strategy and response to elevated atmospheric CO_2 .

KEYWORDS: ENRICHMENT, POPLAR CLONES, SEEDLINGS, SOIL, TEMPERATURE

349

Ceulemans, R., X.N. Jiang, and B.Y. Shao. 1995. Growth and physiology of one-year-old poplar (*populus*) under elevated atmospheric CO_2 levels. *Annals of Botany* 75(6):609-617.

The effects of elevated atmospheric CO_2 concentrations on the ecophysiological responses (gas exchange, chlorophyll a fluorescence, Rubisco activity, leaf area development) as well as on the growth and biomass production of two poplar clones (i.e. *Populus trichocarpa* x *P. deltoides* clone Beaupre and *P. x euramericana* clone Robusta) were examined under open top chamber conditions. The elevated CO_2 treatment (ambient + 350 $\mu\text{mol mol}^{-1}$) stimulated above-ground biomass of clones Robusta and Beaupre after the first growing season by 55 and 38 %, respectively. This increased biomass production under elevated CO_2 was associated with a significant increase in plant height, the latter being the result of enhanced internode elongation rather than an increased production of leaves or internodes. Both an increased leaf area index (LAI) and a stimulated net photosynthesis per unit leaf contributed to a significantly higher stem biomass per unit leaf area, and thus to the increased above-ground biomass production under the elevated CO_2 concentrations in both clones. The larger LAI was caused by a larger individual leaf size and leaf growth rate; the number of leaves was not altered by the elevated CO_2 treatment. The higher net leaf photosynthesis was the result of an increase in the photochemical (maximal chlorophyll fluorescence F_m and photochemical efficiency

Fv/Fm) as well as in the biochemical (increased Rubisco activity) process capacities. No significant differences were found in dark respiration rate, neither between clones nor between treatments, but specific leaf area significantly decreased under elevated CO₂ conditions. (C) 1995 Annals of Botany Company

KEYWORDS: BRANCH BAG, CARBON DIOXIDE, CLONES, ENRICHMENT, GAS-EXCHANGE, LEAF-AREA, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, RESPONSES, WATER-STRESS

350

Ceulemans, R., and M. Mousseau. 1994. Tansley review no-71 - effects of elevated atmospheric CO₂ on woody-plants. *New Phytologist* 127(3):425-446.

Because of their prominent role in the global carbon balance and their possible carbon sequestration, trees are very important organisms in relation to global climatic changes. Knowledge of these processes is the key to understanding the functioning of the whole forest ecosystem which can be modelled and predicted based on the physiological process information. This paper reviews the major methods and techniques used to examine the likely effects of elevated CO₂ on woody plants, as well as the major physiological responses of trees to elevated CO₂. The available exposure techniques and approaches are described. An overview table with all relevant literature data over the period 1989-93 summarizes the percent changes in biomass, root/shoot ratio, photosynthesis, leaf area and water use efficiency under elevated CO₂. Interaction between growth, photosynthesis and nutrition is discussed with a special emphasis on downward regulation of photosynthesis. The stimulation or reduction found in the respiratory processes of woody plants are reviewed, as well as the effect of elevated CO₂ on stomatal density, conductance and water use efficiency. Changes in plant quality and their consequences are examined. Changes in underground processes under elevated CO₂ are especially emphasized and related to the functioning of the ecosystem. Some directions for future research are put forward.

KEYWORDS: BETULA-PENDULA ROTH, BLACK SPRUCE SEEDLINGS, CARBON-DIOXIDE ENRICHMENT, CASTANEA-SATIVA MILL, INSECT HERBIVORE INTERACTIONS, LIRIODENDRON-TULIPIFERA L, LOBLOLLY-PINE SEEDLINGS, SITCHENSIS BONG CARR, SOUR ORANGE TREES, SOURCE-SINK RELATIONS

351

Ceulemans, R., and M. Mousseau. 1995. Effects of elevated atmospheric CO₂ on woody-plants (vol 12m, pg 425, 1995). *New Phytologist* 129(3):535.

352

Ceulemans, R., B.Y. Shao, X.N. Jiang, and J. Kalina. 1996. First- and second-year aboveground growth and productivity of two Populus hybrids grown at ambient and elevated CO₂. *Tree Physiology* 16(1-2):61-68.

Two hybrid poplar (Populus) clones (the fast-growing clone Beaupre (P trichocarpa Torr. and Gray x P. deltoides Bartr. ex Marsh.) and the slow-growing clone Robusta (P deltoides Bartr. ex Marsh. x P. nigra L.)) were grown from hardwood cuttings for one or two growing seasons (1993-1994) in either ambient or elevated (= ambient + 350 $\mu\text{mol mol}^{-1}$) CO₂ in open-top chambers at the University of Antwerpen. Both clones responded positively to the elevated CO₂ treatment with increased stem volume and aboveground biomass production; however, the clones

exhibited different response strategies to the elevated CO₂ treatment, and the responses varied with cutting age and duration of exposure. Clone Beaupre responded to the elevated CO₂ treatment with increases in leaf area and leaf area index during both the first and second growing seasons, but little increase in height growth. Clone Robusta exhibited increased height growth, leaf biomass and total leaf nitrogen content in response to elevated CO₂, but no increase in leaf area index. The elevated CO₂ treatment increased the total number of branches and total branch biomass in both clones during both growing seasons. At the end of the first growing season, woody stem biomass of the fast- and slow-growing clones was increased by 38 and 55%, respectively. At the end of the second growing season, stem volume was increased by 43% in clone Beaupre and by 58% in clone Robusta. The increase in stem volume was a result of the stimulation of both height and diameter growth in the slow-growing clone, whereas only height growth was stimulated in the fast-growing clone. In the fall of the first growing season, the average date of bud set in clone Robusta was advanced by 4 days in the elevated CO₂ treatment; there were no other significant effects of the elevated CO₂ treatment on bud set. The elevated CO₂ treatment enhanced leaf C/N ratios in both clones in both years.

KEYWORDS: ATMOSPHERIC CO₂, CARBONDIOXIDE, CASTANEA-SATIVA MILL, CLONES, ENRICHMENT, GAS-EXCHANGE, PLANTS, RESPONSES, SEEDLINGS, TREES

353

Ceulemans, R., G. Taylor, C. Bosac, D. Wilkins, and R.T. Besford. 1997. Photosynthetic acclimation to elevated CO₂ in poplar grown in glasshouse cabinets or in open top chambers depends on duration of exposure. *Journal of Experimental Botany* 48(314):1681-1689.

The effects of elevated CO₂ were studied on the photosynthetic gas exchange behaviour and leaf physiology of two contrasting poplar (Populus) hybrids grown and treated in open top chambers (OTCs in Antwerp, Belgium) and in closed glasshouse cabinets (GHCs in Sussex, UK). The CO₂ concentrations used in the OTCs were ambient and ambient +350 $\mu\text{mol mol}^{-1}$, while in the GHCs they were c. 360 $\mu\text{mol mol}^{-1}$ versus 719 $\mu\text{mol mol}^{-1}$. Measurements of photosynthetic gas exchange were made for euramerican and interamerican poplar hybrids in combination with measurements of dark respiration rate and Rubisco activity. Significant differences in the leaf anatomy and structure (leaf mass per area and chlorophyll content) were observed between the leaves grown in the OTCs and those grown in the GHCs. Elevated CO₂ stimulated net photosynthesis in the poplar hybrids after 1 month in the GHCs and after 4 months in the OTCs, and there was no evidence of downward acclimation (or downregulation) of photosynthesis when the plants in the two treatments were measured in their growth CO₂ concentration. There was also no evidence of downregulation of Rubisco activity and there were even examples of increases in Rubisco activity. Rubisco exerted a strong control over the light-saturated rate of photosynthesis, which was demonstrated by the close agreement between observed net photosynthetic rates and those that were predicted from Rubisco activities and Michaelis-Menten kinetics. After 17 months in elevated CO₂ in the OTCs there was a significant loss of Rubisco activity for one of the hybrid clones, i.e. Beaupre, but not for clone Robusta. The effect of the CO₂ measurement concentration (i.e. the short-term treatment effect) on net photosynthesis was always larger than the effect of the growth concentration in both the OTCs or GHCs (i.e. the long-term growth CO₂ effect), with one exception. For the interamerican hybrid Beaupre dark respiration rates in the OTCs were not significantly affected by the elevated CO₂ concentrations. The results suggest that for rapidly growing tree species, such as poplars, there is little evidence for downward acclimation of photosynthesis when plants are exposed to elevated CO₂ for up to 4 months; longer term exposure reveals loss of Rubisco activity.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, GAS-

EXCHANGE, HYBRID POPLAR, LEAF DEVELOPMENT, LONG-TERM ELEVATION, POPULUS- EURAMERICANA, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE, TOMATO

354

Ceulemans, R., L. Vanpraet, and X.N. Jiang. 1995. Effects of CO₂ enrichment, leaf position and clone on stomatal index and epidermal-cell density in poplar (populus). *New Phytologist* 131(1):99-107.

The effects of CO₂ enrichment and leaf position on stomatal characteristics (stomatal density, stomatal index and stomatal pore length) and epidermal cell density were examined for two different Populus clones, Beaupre and Robusta, grown from cuttings in open-top chambers under ambient and elevated atmospheric CO₂ conditions. Both clones had amphistomatous leaves, and stomatal density was significantly larger on the abaxial leaf surface than on the adaxial. Significant interactions between CO₂ enrichment, leaf position and clone were observed for most stomatal and epidermal characteristics. A significant reduction of the number of stomata mm⁻² under elevated CO₂ was observed in expanding leaves near the upper portion of the plant for both leaf surface sides and in both clones. For the abaxial leaf side only, this reduction under elevated CO₂ was accompanied by a similar reduction of the stomatal index in both clones. In mature leaves on the middle and lower portion of the plants, there was no significant effect of the CO₂ treatment on stomatal density. In young, expanding leaves near the upper part of the plant there were significant interactions between the CO₂ treatment and leaf surface side for epidermal cell density. The latter increased under elevated CO₂ at the abaxial leaf surface, but decreased at the adaxial surface on the upper part of the plant. Total epidermal cell numbers of mature, fully expanded leaves increased under elevated CO₂ in both clones. The observation that interactions with leaf age and/or leaf position significantly confound the CO₂ treatment effect on stomatal and epidermal cell densities, might contribute to the elucidation of the problem of the phenomenon of stomatal density reduction under elevated atmospheric CO₂.

KEYWORDS: ANATOMY, ATMOSPHERIC CO₂, GROWTH, INCREASE, NUMBERS, OAK LEAVES, TEMPERATURE

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Chabot, S., R. Belrhid, R. Chenevert, and Y. Piche. 1992. Hyphal growth promotion invitro of the va mycorrhizal fungus, gigasporamargarita becker and hall, by the activity of structurally specific flavonoid compounds under CO₂-enriched conditions. *New Phytologist* 122(3):461-467.

Plant phenolic compounds are known to be inducers of virulence genes in plant-pathogen interactions such as those involving Agrobacterium, and flavonoids are known to be inducers or inhibitors of Nod genes in Rhizobium-legume symbiosis. More recent studies suggest that some of these compounds act as molecular signals in the development of vesicular-arbuscular mycorrhizas (VAM). The present study has shown that hyphal growth of the VAM fungus, Gigaspora margarita Becker & Hall, is affected by both stimulatory and inhibitory flavonoids, when applied at 10 μM together with an optimal carbon dioxide enrichment. Stimulatory compounds were all flavonols (kaempferol, quercetin and morin) and possessed at least one hydroxyl group on the B ring. Conversely, two isoflavones (biochanin A, and genistein), a single flavanone (hesperetin) and two compounds without any hydroxyl group on the B ring, galangin (flavonol) and chrysin (flavone), were all inhibitors of hyphal growth.

KEYWORDS: AGROBACTERIUM-TUMEFACIENS, DNA TRANSFORMED ROOTS, EXPRESSION, HOST, IDENTIFICATION, MELILOTI NODULATION GENES, PHENOLIC-COMPOUNDS, RHIZOBIUM, SIGNAL COMPOUNDS, SPORE GERMINATION

356

Chagvardieff, P., T. Daletto, and M. Andre. 1994. Specific effects of irradiance and CO₂ concentration doublings on productivity and mineral-content in lettuce. *Life Sciences and Space Research XXV (3) 14(11):269-275.*

Experiments in growth chambers with controlled atmosphere were performed to compare the effects on the productivity of two treatments stimulating photosynthesis : the doubling of CO₂ concentration, the doubling of irradiance; the combining of both was also tested. A large effect of light was noticed : (i) the accumulation of carbon was, contrarily to CO₂ effect, amplified within time, and led to the most important dry matter production. (ii) the specific leaf weight was about two-fold increased. (iii) the nitrate content was 2-3 fold less. A significant positive effect of CO₂ was detected on the fresh biomass production and the iron content of lettuce. A synergy was observed on dry matter production by the interaction of the two factors.

KEYWORDS: CARBOHYDRATE, ENRICHMENT, GROWTH, HIGH-PRESSURE SODIUM, LAMPS, LIGHT, PHOTOSYNTHESIS

357

Chagvardieff, P., B. Dimon, A. Souleimanov, D. Massimino, S. Le Bras, M. Pean, and D. Louche-Teissandier. UNKNOWN YEAR. Effects of modified atmosphere on crop productivity and mineral content. *Life Sciences: Life Support Systems Studies-I :1971-1974.*

Wheat, potato, pea and tomato crops were cultivated from seeding to harvest in a controlled and confined growth chamber at elevated CO₂ concentration (3700 μ L.L-1) to examine the effects on biomass production and edible part yields. Different responses to high CO₂ were recorded, ranging from a decline in productivity for wheat, to slight stimulation for potatoes, moderate increase for tomatoes, and very large enhancement for pea. Mineral content in wheat and pea seeds was not greatly modified by the elevated CO₂. Short-term experiments (17 d) were conducted on potato at high (3700 μ L.L-1) and very high (20,000 μ L.L-1) CO₂ concentration and/or low O₂ partial pressure (similar to 20,600 μ L.L-1 or 2 kPa). Low O₂ was more effective than high CO₂ in total biomass accumulation, but development was affected: Low O₂ inhibited tuberization, while high CO₂ significantly increased production of tubers. (C) 1997 COSPAR. Published by Elsevier Science Ltd.

KEYWORDS: INCOMPLETE, CARBON DIOXIDE, CO₂ CONCENTRATION, GROWTH, IRRADIANCE, POTATO, TEMPERATURE, WHEAT

358

Chalabi, Z., and J.E. Fernandez. 1992. Spatiotemporal responses of a glasshouse to gaseous enrichment. *Journal of Agricultural Engineering Research* 51(2):139-151.

KEYWORDS: SUMMER CO₂ ENRICHMENT, SYSTEMS, YIELD

359

Chalabi, Z.S., and J.E. Fernandez. 1994. Estimation of net photosynthesis of a greenhouse canopy using a mass-balance method and mechanistic models. *Agricultural and Forest Meteorology* 71(1-2):165-182.

Two mechanistic models for estimating net photosynthesis of a greenhouse canopy are evaluated against measurements using mass balance of CO₂ fluxes. The discrepancies observed between the mechanistic models and the CO₂ mass balance measurement method are

attributed to the underestimation of leakage rate, the error in estimating radiation transmission in direct light conditions, and the spatial inhomogeneity of the CO₂ concentration inside the glasshouse.

KEYWORDS: CO₂- ENRICHMENT, CROP, OPTIMIZATION, STRATEGY, VENTILATION

360

Chan, Y.S.G., M.H. Wong, and B.A. Whitton. 1998. Effects of landfill gas on growth and nitrogen fixation of two leguminous trees (*Acacia confusa*, *Leucaena leucocephala*). *Water, Air, and Soil Pollution* 107(1-4):409-421.

A study was made on the effects of landfill gas on ARA (acetylene reducing activity) of nodules of two woody legumes (*Acacia confusa* and *Leucaena leucocephala*) widespread on landfill sites in Hong Kong. The effects of the three main components of landfill gas, O₂, CO₂ and CH₄, were first measured separately over a 1-hr period. Maximum ARA was found at 20% O₂ (close to atmospheric partial pressure) and ARA decreased as the O₂ decreased in the range of 16-1%. *Acacia confusa* nodular ARA was significantly inhibited at 30-50% CO₂, but not *Leucaena leucocephala* nodular ARA. CH₄ had no significant effect on ARA of either species. As the landfill gas concentrations in the landfill topsoil were mostly > 10% O₂ and < 10% CO₂, root nodules should fix N₂ effectively over these ranges of gases. A four-week test was conducted to assess the long-term influence of landfill gas on seedlings of the two legumes. Landfill gas and elevated CO₂ both suppressed their growth and their nodular ARA. Even under the influence of the gases, however, seedlings with nodules formed a higher biomass than seedlings lacking nodules. The growth of the two legumes under actual landfill conditions was investigated by transplanting non-inoculated and pre-inoculated seedlings to two landfill sites in Hong Kong: Junk Bay and Shuen Wan Landfill. After six months, most of the non-inoculated seedlings became infected: *Acacia confusa* 63 and 70%, *Leucaena leucocephala* 17 and 89%, respectively, at the test sites. The results indicate that there were free rhizobia at these landfill sites to infect the legumes and they had formed effective nodules to fix N₂ under landfill conditions.

KEYWORDS: CARBON DIOXIDE, NODULES, PLANTS

361

Chapin, F.S., E. Rincon, and P. Huante. 1993. Environmental responses of plants and ecosystems as predictors of the impact of global change. *Journal of Biosciences* 18(4):515-524.

An understanding of plant responses to fluctuations in environment is critical to predictions of plant and ecosystem responses to climate change. In the northern hemisphere, the northern limits of distribution of major biomes are probably determined by the tolerance of their dominant physiognomic types (e.g., deciduous hardwood trees) to minimum winter temperatures and can thus be predicted from long-term patterns of temperature fluctuations. At a more detailed level, the responses of functional groups of plants to altered climate can be predicted from their known responses to fluctuations in soil resources (nutrients and water) and the expected effect of climatic change on these soil resources. Laboratory and field experiments demonstrate the feasibility of this approach.

KEYWORDS: CO₂-INDUCED CLIMATE CHANGE, CONTRASTED ECOLOGY, ENRICHMENT, FOREST, GROWTH, MEXICO, NORTH-AMERICA, PLASTICITY, ROOT-SYSTEM, SEEDLINGS

362

Chaves, M.M., and J.S. Pereira. 1992. Water-stress, CO₂ and climate

change. *Journal of Experimental Botany* 43(253):1131-1139.

Climatic change may bring about increased aridity to large areas of Europe. Higher temperatures, larger water deficits and high light stress are likely to occur in conjunction with elevated atmospheric CO₂. This raises the question whether a high CO₂ concentration in the atmosphere can compensate for the decrease in carbon gain in water-stressed plants. The processes which determine dry matter production and the ways they are affected by soil water deficits are discussed. It is now well established that in most species and under most circumstances stomata are the main limiting factor to carbon uptake under water deficit, the photosynthetic machinery being highly resistant to dehydration. However, when other stresses are superimposed, a decline in photosynthetic capacity may be observed. In the short term, under drought conditions, the increase in CO₂ in the atmosphere may diminish the importance of stomatal limitation for carbon assimilation, inhibit photorespiration, stimulate carbon partitioning to soluble sugars and increase water-use efficiency. Some recent evidence seems to indicate that under conditions of high irradiance, plants growing at elevated CO₂ may develop protection towards photoinhibition, which might otherwise result in significant losses in plant production under stress conditions. In the longer term though, a negative acclimation of photosynthesis appears to occur in many species, an explanation for which still needs to be clearly identified. Similarly, the effects of extended exposure to elevated CO₂ under arid conditions are not known. Plant production is more closely related to the integral of photosynthesis over time and total foliage area than to the instantaneous rates of the photosynthetic process. Water deficits result in a decrease in foliage area biomass and, therefore, in productivity. On the other hand, the increase in air temperature may result in more respiratory losses. However, experimental as well as simulatory evidence suggests that doubling CO₂ concentration in the air may improve carbon assimilation and compensate partially for the negative effects of water stress even if we assume a down-regulation of the photosynthetic process as a result of acclimation to elevated CO₂.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DROUGHT STRESS, DRY-WEIGHT, ELEVATED CO₂, LONG-TERM EXPOSURE, *PHASEOLUS-VULGARIS* L, PHOTOSYNTHETIC INHIBITION, RIBULOSE BIPHOSPHATE CARBOXYLASE, STOMATAL DENSITY, SUCROSE PHOSPHATE SYNTHASE

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Chaves, M.M., J.S. Pereira, S. Cerasoli, J. CliftonBrown, F. Miglietta, and A. Raschi. 1995. Leaf metabolism during summer drought in *Quercus ilex* trees with lifetime exposure to elevated CO₂. *Journal of Biogeography* 22(2-3):255-259.

A marginal improvement in the response of *Quercus ilex* adult trees to drought appears to occur under a long-term natural CO₂ enrichment. This is expressed, for example, by the absence of midday stomatal closure in trees growing under elevated CO₂. Some protection against high irradiance and high temperature seems also to occur at the photochemical level, presumably as a result of more carbon available to the consumption of excess light energy. This would allow a better performance of the plants grown under elevated CO₂ during the warmer hours of the day and therefore playing an important adaptation role under drought conditions. A marginal increase in the concentration of soluble sugars and starch was observed in the leaves of trees growing at elevated CO₂ as compared with plants at ambient CO₂, mainly during the midday hours. We may speculate that this will be advantageous both in terms of carbohydrate reserves for growth (e.g. more roots) and osmotic adjustment.

KEYWORDS: FIELD, LEAVES, QUANTUM YIELD

364

Chemeris, Y.K., L.V. Shenderova, and P.S. Venediktov. 1996. Chloroplast respiration in *Chlorella pyrenoidosa* CALU-175: Effects of nitrogen deficiency, exogenous glucose, and elevated temperature. *Russian Journal of Plant Physiology* 43(4):474-479.

The rate of chloroplast respiration in *Chlorella* was studied with respect to some changes in the physiological state induced by nitrogen deficiency, heterotrophic growth, and incubation at supraoptimal temperature. Iodoacetamide (an inhibitor of glycolysis), salicylhydroxamate (an inhibitor of nonmitochondrial respiration), and 2-deoxy-D-glucose (a nonmetabolizable analogue of glucose), inhibited the respiration of chloroplasts. Treatments that inactivate photosystem II (PS II), i.e., the addition of glucose, nitrogen deprivation, or dark incubation at elevated temperatures (39-43 degrees C), drastically (8-10 times) increased the rate of chloroplast respiration. In the absence of CO₂, no enhancement of chloroplast respiration was recorded in nitrogen-starved cells. Cycloheximide, an inhibitor of cytoplasmic protein synthesis, and 2-deoxy-D-glucose prevented the increase in the chloroplast respiration rate caused by the addition of glucose or incubation at elevated temperatures. It is suggested that the inhibition of PS II, previously described in *Chlorella* incubated for a long time at supraoptimal temperature, is associated with the enhancement of chloroplast respiration.

KEYWORDS: CELLS, CHLAMYDOMONAS-REINHARDTII, CHLORORESPIRATION, TRANSPORT

365

Chemeris, Y.K., P.S. Venediktov, and A.B. Rubin. 1996. Role of chloroplast respiration in the inactivation of photosystem II in *Chlorella*. *Russian Journal of Plant Physiology* 43(6):716-723.

Nitrogen deficiency, dark incubation on glucose, and dark incubation at an elevated temperature (41 degrees C) were previously shown to inactivate photosystem II (PS II) in *Chlorella pyrenoidosa* Chick, strain CALU-175. These treatments also increased chloroplast respiration by 7-11 times. At the same time, any attempt to inhibit the accumulation of substrates for chloroplast respiration (CO₂ deprivation during nitrogen starvation, inhibition of glucose metabolism by a nonmetabolizable analog of glucose, 2-deoxy-D-glucose, or inhibition of protein synthesis by cycloheximide during dark incubation on glucose or by heat shock) prevented the stimulation of chloroplast respiration and PS II inactivation. Inhibition of the oxygen-dependent oxidation of the plastoquinone pool under anaerobic conditions or in the presence of salicylhydroxamate, an inhibitor of chloroplast oxidases, markedly increased the extent and rate of PS II inactivation in cells subjected to heat shock. The dependencies of chloroplast respiration and the PS II inactivation rate on the heat-shock temperature exactly matched one another. Diuron, an inhibitor of photosynthetic electron transport between the primary and secondary quinone electron acceptors, did not affect the rate of chloroplast respiration, but prevented PS II inactivation. We propose that the inactivation of PS II caused by these treatments is due to the loss of the primary quinone electron acceptor as a consequence of its two-electron reduction from the plastoquinone reduced by the electron flow from the substrates of chloroplast respiration.

KEYWORDS: CHLAMYDOMONAS-REINHARDTII, CHLORORESPIRATION

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Chen, C.L., C.C. Li, and J.M. Sung. 1994. Carbohydrate-metabolism enzymes in CO₂-enriched developing rice grains of cultivars varying in grain-size. *Physiologia Plantarum* 90(1):79-85.

The increased supply of photosynthate from maternal tissue is known to

promote grain growth in several crop species. However, the effect of increasing photosynthate supply on grain growth receives little attention in rice. This study was aimed at evaluating the effect of increasing photosynthate supply through CO₂ enrichment (650 μmol l⁻¹) on grain growth in three rice cultivars differing in grain size. CO₂ enrichment was applied to the pot-grown plants between anthesis and final harvest. The results indicated that high CO₂ treatment enhanced the CO₂ exchange rate of leaf tissue, and subsequently increased the sucrose level of peduncle exudate, but it did not promote starch accumulation in the developing grains. This phenomenon was linked to the poor CO₂ responses for the grain activities of sucrose synthase, UDP-glucose pyrophosphorylase, ADP-glucose pyrophosphorylase, and starch synthases involved in the conversion of sucrose to starch. Significant cultivar differences also existed for the activities of sucrose to starch conversion enzymes with larger grain size cultivars tending to have higher enzyme activities (expressed on a grain basis), resulting in a greater carbohydrate accumulation.

KEYWORDS: ACCUMULATION, CARBON DIOXIDE, CO₂, GROWTH, MAIZE, ORYZA-SATIVA, STARCH, SUCROSE SYNTHASE, ULTRAVIOLET-B RADIATION, WHEAT

367

Chen, C.T., and T.L. Setter. 1997. Potato response to elevated CO₂ and temperature. *Plant Physiology* 114(3):490.

368

Chen, D.X., and M.B. Coughenour. 1996. A mechanistic model for submerged aquatic macrophyte photosynthesis: *Hydrilla* in ambient and elevated CO₂. *Ecological Modelling* 89(1-3):133-146.

There are significant knowledge gaps about the responses of submerged aquatic macrophytes to CO₂ enrichment and global warming. A mechanistic steady-state photosynthesis model for submerged aquatic macrophytes was developed to provide an analysis tool to investigate the responses of plant photosynthesis to CO₂, temperature and light. The model was based upon a general simplified scheme for inorganic carbon assimilation of submerged aquatic macrophytes which integrated the knowledge about aquatic plant photosynthesis from previous research, mainly on *Hydrilla*. The model includes: (1) diffusion and/or active transfer of inorganic carbon (CO₂ and/or HCO₃⁻) in the bathing medium into the leaf mesophyll and cytosol; (2) diffusion and/or 'pumping' of CO₂ through the PEPcase-related C-4 pathway into the chloroplast; (3) inter-conversions between CO₂ and HCO₃⁻ inside cells; (4) photosynthetic carbon reduction cycle (PCR) in the chloroplast. In the model, the PCR processes in the chloroplast were described using the widely accepted C-3 photosynthesis model. The activity of the C-4 cycle was related to environmental CO₂ 'stress'. In this way, the model can simulate the shift between C-3-like and C-4-like photosynthesis under different environmental conditions. The model was validated using gas exchange data from *Hydrilla* plants grown in ambient and elevated CO₂. The model predicted quite well photosynthetic responses to incident PAR, temperature and ambient CO₂ for both ambient and elevated atmospheric CO₂ treatments. Model predictions agreed well with measured *Hydrilla* gas exchange data. The simulated and measured CO compensation points of *Hydrilla* leaf photosynthesis were about 100 ppm. The light compensation point of photosynthesis was about 25 μmol m⁻²s⁻¹ (PAR), and photosynthesis rate was saturated at about 100 μmol m⁻²s⁻¹ (PAR). Higher pH slightly increased photosynthesis rates at ambient CO₂ (similar to 350 ppm). There was no significant acclimation of *Hydrilla* photosynthesis to elevated CO₂ within the experimental period. Simulated CO₂ compensation point decreased with increasing activity of C-4-cycle processes.

KEYWORDS: ASSIMILATION, CARBOXYLASE, FIXATION, LEAVES,

369

Chen, D.X., M.B. Coughenour, D. Eberts, and J.S. Thullen. 1994. Interactive effects of CO₂ enrichment and temperature on the growth of dioecious hydrilla-verticillata. *Environmental and Experimental Botany* 34(4):345-353.

Experiments of plant growth responses to different CO₂ concentrations and temperatures were conducted in growth chambers to explore the interactive effects of atmospheric CO₂ enrichment and temperature on the growth and dry matter allocation of dioecious Hydrilla [Hydrilla verticillata (L.f.) Royle]. Hydrilla plants were exposed to two atmospheric CO₂ concentrations (350 and 700 ppm) and three temperatures (15, 25 and 32 degrees C) under a 12-hr photoperiod for about 2 months. The plant growth analysis showed that elevated CO₂ appeared to enhance the growth of Hydrilla, and that the percentage of the enhancement is strongly temperature-dependent. Maximum biomass production was achieved at 700 ppm CO₂ and 32 degrees C. At 15 degrees C, the total dry matter production was increased about 27% by doubling CO₂, due to a 26% enhancement of leaf biomass, a 34% enhancement of stem biomass and 16% enhancement of root biomass. At 25 degrees C, the dry matter production was increased about 46% by doubling CO₂, due to a 29% enhancement of leaf biomass, a 27% enhancement of stem biomass and 40% enhancement of root biomass. At 32 degrees C, however, the percentage of the enhancement of total dry matter production by doubling CO₂ was only about 7%. The dry matter allocation among different plant parts was influenced by temperature but not by elevated CO₂ concentration.

KEYWORDS: AQUATIC MACROPHYTES, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO₂, ENVIRONMENT, PHOTOSYNTHETIC RESPONSE, YIELD

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Chen, D.X., M.B. Coughenour, A.K. Knapp, and C.E. Owensby. 1994. Mathematical simulation of C₄ grass photosynthesis in ambient and elevated CO₂. *Ecological Modelling* 73(1-2):63-80.

A mechanistic leaf photosynthesis model was developed for C₄ grasses based on a general simplified scheme of C₄ plant carbon metabolism. In the model, the PEPcase-dependent C₄-cycle was described in terms of CO₂ concentration in the mesophyll space using Michaelis-Menten kinetics, and the activity of PEPcase was related to the incident PAR to take account of the influence of light on the activity of C₄-cycle processes. The CO₂ refixation by Rubisco in the bundle sheath was described using a widely accepted C₃ photosynthesis model. The model assumes a steady state balance among CO₂ diffusion from surrounding atmosphere into the mesophyll space, CO₂ transport into the bundle sheath by the C₄-cycle, CO₂ refixation by the C₃-cycle in the bundle sheath, and CO₂ leakage from the bundle sheath. The response to temperature of photosynthesis was incorporated via the temperature dependence of model parameters. The photosynthesis model was coupled with a stomatal conductance model in order to predict leaf photosynthesis rates at different atmospheric conditions. The empirical model of Ball et al. (1987) was adopted and slightly modified to describe responses in stomatal conductance. The coupled model was parameterized for the C₄ grass *Andropogon gerardii* grown in both ambient (350 ppm) and elevated (700 PPM) CO₂ atmospheres. The key parameters of the model were estimated by fitting the model to the measured data using non-linear regression. The model was validated by comparison the predicted photosynthetic response to PAR in both CO₂-pretreatments with the measured data from an independent gas exchange experiment. The predicted photosynthesis and stomatal conductance matched the measured data quite well for both atmospheric CO₂-pretreatments. At 25-degrees-C, the estimated maximum carboxylation

rate of Rubisco $V_{(m,25)}$, potential electron transport rate $J_{(m,25)}$ and quantum efficiency α were increased by CO₂ enrichment. The maximum PEPcase activity $V_{(pm,25)}$ was lower in elevated CO₂. The model predicted that the light-saturated leaf photosynthesis will increase by about 10% with the rising of atmospheric CO₂ from 350 to 700 ppm at 30-degrees-C, and that the optimal temperature of photosynthesis will shift from 37 to 38.5-degrees-C. The estimated slope of the stomatal conductance model was increased by atmospheric CO₂ enrichment. Stomatal conductance was significantly reduced by increasing atmospheric CO₂ concentration.

KEYWORDS: 1,5-BISPHOSPHATE CARBOXYLASE OXYGENASE, BUNDLE SHEATH-CELLS, C-4, INORGANIC CARBON, LEAVES, MECHANISM, MODEL, PLANTS, TALLGRASS PRAIRIE, TEMPERATURE-DEPENDENCE

371

Chen, D.X., H.W. Hunt, and J.A. Morgan. 1996. Responses of a C-3 and C-4 perennial grass to CO₂ enrichment and climate change: Comparison between model predictions and experimental data. *Ecological Modelling* 87(1-3):11-27.

Ecological responses to CO₂ enrichment and climate change are expressed at several interacting levels: photosynthesis and stomatal movement at the leaf level, energy and gas exchanges at the canopy level, photosynthate allocation and plant growth at the plant level, and water budget and nitrogen cycling at the ecosystem level. Predictions of these ecosystem responses require coupling of ecophysiological and ecosystem processes. Version GEM2 of the grassland ecosystem model linked biochemical, ecophysiological and ecosystem processes in a hierarchical approach. The model included biochemical level mechanisms of C-3 and C-4 photosynthetic pathways to represent direct effects of CO₂ on plant growth, mechanistically simulated biophysical processes which control interactions between the ecosystem and the atmosphere, and linked with detailed biogeochemical process submodels. The model was tested using two-year full factorial (CO₂, temperature and precipitation) growth chamber data for the grasses *Panicum smithii* (C-3) and *Bouteloua gracilis* (C-4). The C-3-C-4 photosynthesis submodels fitted the measured photosynthesis data from both the C-3 and the C-4 species subjected to different CO₂, temperature and precipitation conditions. The whole GEM2 model accurately fitted plant biomass dynamics and plant N content data over a wide range of temperature, precipitation and atmospheric CO₂ concentration. Both data and simulation results showed that elevated CO₂ enhanced plant biomass production in both *P. smithii* (C-3) and *B. gracilis* (C-4). The enhancement of shoot production by elevated CO₂ varied with temperature and precipitation. Doubling CO₂ increased modeled annual net primary production (NPP) of *P. smithii* by 36% and 43% under normal and elevated temperature regimes, respectively, and increased NPP of *B. gracilis* by 29% and 24%. Doubling CO₂ decreased modeled net N mineralization rate (N_{min}) of soil associated with *P. smithii* by 3% and 2% at normal and high temperatures, respectively. N_{min} of *B. gracilis* soil decreased with doubled CO₂ by 5% and 6% at normal and high temperatures. NPP increased with precipitation. The average NPP and N_{min} of *P. smithii* across the treatments was greater than that of *B. gracilis*. In the C-3 species the response of NPP to increased temperatures was negative under dry conditions with ambient CO₂, but was positive under wet conditions or doubled CO₂. The responses of NPP to elevated CO₂ in the C-4 species were positive under all temperature and precipitation treatments. N_{min} increased with precipitation in both the C-3 and C-4 species. Elevated CO₂ decreased N_{min} in the C-4 system. The effects of elevated CO₂ on N_{min} in the C-3 system varied with precipitation and temperature. Elevated temperature decreased N_{min} under dry conditions, but increased it under wet conditions. Thus, there are strong interactions among the effects of CO₂ enrichment, precipitation, temperature and species on NPP and N_{min}. Interactions between ecophysiological processes and ecosystem

processes were strong. GEM2 coupled these processes, and was able to represent the interactions and feedbacks that mediate ecological responses to CO₂ enrichment and climate change. More information about the feedbacks between water and N cycling is required to further validate the model. More experimental and modeling efforts are needed to address the possible effects of CO₂ enrichment and climate change on the competitive balance between different species in a plant community and the feedbacks to ecosystem function.

KEYWORDS: AMBIENT, CARBON, ELEVATED ATMOSPHERIC CO₂, GROWTH, LEAVES, PLANTS, RISING CO₂, SIMULATION-MODEL, TEMPERATURE-DEPENDENCE, WATER-USE

372

Chen, J.L., and J.F. Reynolds. 1997. GePSi: A generic plant simulator based on object-oriented principles. *Ecological Modelling* 94(1):53-66.

The Generic Plant Simulator (GePSi) is a physiologically-based model that combines modules for canopy, root environment, water relations, and potential growth to generate whole-plant carbon, nitrogen, and water balances. The version presented here is coded in the object-oriented programming (OOP) language, C++, to enhance the implementation of modularity. In the aboveground aerial environment, the Weather module defines the weather conditions above a canopy, and MicroWeather defines the vertical profiles of micro-meteorological variables in a canopy. The belowground soil environment contains the SoilProperty modules, which define vertical profiles of physical and chemical variables in a soil column. The 'part-of' hierarchy in GePSi follows the structure of a real plant: the Plant module calls canopy and root system modules; the Canopy module, in turn, calls leaf, stem and fruit modules, and the RootSystem module calls coarse and fine root modules, etc. Our long-term goal is for GePSi to serve as a template for building a plant growth simulator by simply selecting appropriate modules for the question being asked. We are building a suite of plant modules (and their interfaces) based on general principles that are fundamentally similar for different kinds of plants. This includes photosynthesis, growth, nutrient and carbon allocation, water uptake, etc. These modules can be parameterized for specific species, related groups of species, life-forms, or broader groups depending on how variable the processes are across the groupings and the amount of unexplained variability that is acceptable for the question being investigated. Our modular-based approach has numerous advantages, including improving the understanding of the model, reducing duplication of effort, and facilitating the adaptation of the model for different sites and ecosystems. (C) 1997 Elsevier Science B.V.

KEYWORDS: DESIGN, ECOLOGICAL MODEL, GROWTH, SYSTEMS

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Chen, K., G.Q. Ha, N. Keutgen, M.J.J. Janssens, and F. Lenz. 1999. Effects of NaCl salinity and CO₂ enrichment on pepino (*Solanum muricatum* Ait.) - I. Growth and yield. *Scientia Horticulturae* 81(1):25-41.

One-month old, rooted, semi-hardwood cutting plants of pepino cv. Xotus in sand-potted culture were treated with 200 ml Hoagland nutrient solution with or without additional 25 mM NaCl twice a week for 2 months, and exposed to 350 +/- 10, 700 +/- 10 or 1050 +/- 10 ppm CO₂ in controlled environment chambers during the last month of the experiment. NaCl salinity in the rhizosphere reduced growth of all the organs, but raised stem dry weight ratio and root dry weight ratio. In contrast, atmospheric CO₂ enrichment increased plant and fruit growth. Leaf dry weight ratio and fruit dry weight ratio rose, but stem dry weight ratio and root dry weight ratio decreased at high CO₂ levels. Daily expansion rate of leaf area, growth rate of side-shoot length, rate of plant dry mass production, and increased rate of fresh fruit weight decreased

due to NaCl stress, but increased with CO₂ enrichment. Side-shoot diameter rose, whereas specific leaf area, leaf area ratio, and side-shoot dry weight ratio declined under both NaCl-stressed and CO₂-enriched conditions. In comparison with the 350 ppm CO₂ treatment without NaCl salinity in the rhizosphere, net assimilation rate and relative growth rate of plants were reduced by 8-13% and 16-32% due to NaCl salinity, and enhanced by 22-23% and 42-64% at 700 ppm CO₂, and by 36-44% and 64-101% at 1050 ppm CO₂, respectively. The simultaneous treatments of NaCl salinity and high CO₂ resulted in indefinite effects on vegetative and reproductive growth as well as on dry mass production of different plant organs. Nevertheless, the negative impacts of NaCl stress on plant growth and fruit yield diminished at high CO₂ levels. Atmospheric CO₂ enrichment increased the tolerance of pepino to NaCl salinity in the root medium. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CELLS, ECOSYSTEMS, FRUIT, PHOTOSYNTHESIS, PLANTS, RESPONSES

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Chen, K., G.Q. Hu, N. Keutgen, M. Blanke, and F. Lenz. 1997. Effects of CO₂ concentration on strawberry. II. Leaf photosynthetic function. *Journal of Applied Botany-Angewandte Botanik* 71(5-6):173-178.

Two-week-old strawberry (*Fragaria x ananassa* Duch, cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO₂ in controlled environment chambers for 50 days. An elevated CO₂ concentration up to 750 ppm reduced total chlorophyll, chlorophyll a and chlorophyll b contents as well as the a/b ratio. Long-term CO₂ enrichment induced leaf senescence and decreased photosynthetic efficiency as well as photochemical conversion efficiency of PS II. Intercellular CO₂ concentration significantly increased with CO₂ enrichment. Stomatal conductance, transpiration rate, and net photosynthesis rate of young leaves increased with raising CO₂ concentrations. However, CO₂ levels above 600 ppm markedly reduced net photosynthetic rate of adult and old leaves. High CO₂ concentrations up to 900 ppm did not significantly affect dark respiration rate of the leaves. Photosynthetic water-use efficiency was highest in old leaves and lowest in young ones. Increased CO₂ concentrations up to 600-750 ppm improved leaf photosynthetic capacity by increasing photosynthetic water-use efficiency.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, PLANTS, RESPONSES, WATER-USE

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Chen, K., G.Q. Hu, N. Keutgen, M.J.J. Janssens, and F. Lenz. 1999. Effects of NaCl salinity and CO₂ enrichment on pepino (*Solanum muricatum* Ait.) - II. Leaf photosynthetic properties and gas exchange. *Scientia Horticulturae* 81(1):43-56.

One-month old, rooted semi-hardwood cutting plants of pepino cv. Xotus in sand-potted culture were treated with 200 ml Hoagland nutrient solution with or without additional 25 mM NaCl twice a week for 2 months, and exposed to 350 +/- 10, 700 +/- 10 or 1050 +/- 10 ppm CO₂ in controlled environment chambers during the last month of the experiment. Both NaCl salinity in the rhizosphere and atmospheric CO₂ enrichment reduced the leaf content of total chlorophyll, chlorophyll a and chlorophyll b, as well as stomatal conductance and transpiration rate, but raised intercellular CO₂ concentration and C₂H₄ emission of leaves. Minimal fluorescence yield, maximal fluorescence yield, variable fluorescence yield of dark-adapted leaves, optimal quantum yield and effective quantum yield of PS II, photochemical quenching coefficient, net photosynthetic rate, leaf water-potential, and photosynthetic water-

use efficiency decreased under NaCl stress, but rose with an increase of the atmospheric CO₂ concentration. In addition, the non-photochemical quenching coefficient and the dark respiration rate of leaves increased due to NaCl salinity and decreased at high CO₂ conditions. On average, net photosynthetic rate and photosynthetic water-use efficiency of leaves decreased by 26-35% and 19-29% due to the presence of NaCl stress in the root medium, but increased by 75-98% and 85-123% at 700 ppm CO₂, and by 72-91% and 124-147% at 1050 ppm CO₂ in comparison with 350 ppm CO₂ treatments. Under NaCl stress, high CO₂ improved photosynthetic water-use efficiency of leaves. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, ELEVATED CO₂, GROWTH, RESPIRATION, RESPONSES, STRAWBERRY, STRESS

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Chen, K., G.Q. Hu, N. Keutgen, and F. Lenz. 1997. Effects of CO₂ concentration on strawberry. I. Plant Growth analysis. *Journal of Applied Botany-Angewandte Botanik* 71(5-6):168-172.

Two-week-old strawberry (*Fragaria x ananassa* Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO₂ in controlled environment chambers for 50 days. Elevated CO₂ promoted plant growth as indicated by a higher number of leaves, runners and daughter plants, larger leaf area index and dry mass per unit leaf area, increased total length of runners, plant height, canopy diameter, and enhanced daily growth of leaf area, runner and plant biomass. In contrast, specific leaf area and leaf area ratio of the plants decreased with increasing CO₂ concentration, whereas neither average leaf area nor average runner length was significantly affected by CO₂ enrichment. When compared with the 300 ppm CO₂ treatment, 600 and 900 ppm CO₂-treated plants led to a daily increment of 1.6 and 1.9 total leaf area, 1.1 and 1.8 total runner length, and 2.5 and 3.9 plant biomass, respectively. Increased CO₂ concentration from 300 to 600 and 750 ppm markedly accelerated both relative growth rate and net assimilation rate of the plants. Leaf weight ratio and root weight ratio were significantly higher, while stem weight ratio was significantly lower above 600 ppm CO₂ as a result of proportionally more biomass allocated to leaves and roots than to stems. Apart from an enhancement of plant growth, the long-term CO₂ enrichment boosted vegetative propagation of strawberry plants as well. From an economical point of view, however, it is more efficient to use elevated CO₂ concentrations of up to 600-750 ppm rather than 900 ppm for greenhouse cultivation of strawberry.

KEYWORDS: SCIENCE

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Chen, K., G.Q. Hu, N. Keutgen, and F. Lenz. 1997. Effects of CO₂ concentration on strawberry. III. Dry matter production and water consumption. *Journal of Applied Botany-Angewandte Botanik* 71(5-6):179-182.

Two-week-old strawberry (*Fragaria x ananassa* Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO₂ in controlled environment chambers for 50 days. Elevated CO₂ concentrations enhanced dry matter production, the root/shoot ratio and total water consumption of the plants. High CO₂ promoted total dry matter increment and total leaf area increment of the plants, and improved dry matter- production efficiency and plant water-use efficiency. Water- consumption rate of plants and water-uptake efficiency of roots, however, declined at CO₂-enriched conditions. In comparison with the 300 ppm CO₂ treatment, 600 and 900 ppm CO₂-grown plants increased dry matter-production efficiency by 37 % and 67 %, water-use efficiency by 137 % and 272 %, while reduced water-consumption rate by 39 % and 55 %, and water- uptake efficiency of roots by 53 % and 76 %, respectively. Increasing CO₂ concentrations

from 300 to 900 ppm enabled strawberry plants to produce dry matter more efficiently and to use soil water more economically because it reduced the impact of water stress on plant productivity.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, PLANTS, RESPONSES, ROOTS

378

Chen, K., G.Q. Hu, and F. Lenz. 1997. Effects of CO₂ concentration on strawberry. IV. Carbohydrate production and accumulation. *Journal of Applied Botany-Angewandte Botanik* 71(5-6):183-188.

Two-week-old strawberry (*Fragaria x ananassa* Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO₂ in controlled environment chambers for 50 days. Increasing CO₂ concentration from 300 to 900 ppm promoted carbohydrate production of the plants, and subsequently increased carbohydrate accumulation in the plant organs, especially starch in leaves. Relative distribution of non-structural carbohydrates decreased in leaves and stems at 750 and 900 ppm CO₂, increased in roots from 300 to 750 ppm CO₂. Elevating CO₂ concentration from 300 to 750 ppm reduced the proportions of glucose, fructose, and sucrose, but raised the proportion of starch in non-structural carbohydrates of the plants, as well as increased starch/sucrose ratio in leaves, stems, and whole plants. CO₂ enrichment up to 900 ppm improved carbohydrate-production efficiency of the plants. This effect was particularly pronounced for starch. In comparison with 300 ppm CO₂-grown plants, those treated by 600 and 900 ppm CO₂ raised starch-, glucose-, fructose-, sucrose-, and non- structural carbohydrate-production efficiency by 2.6 and 16.1 fold, 1.6 and 2.1 fold, 0.6 and 1.0 fold, 0.8 and 1.6 fold, and 1.2 and 3.5 fold, respectively.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, ROOTS

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Chen, K., G.Q. Hu, and F. Lenz. 1997. Effects of CO₂ concentration on strawberry. V. Macronutrient uptake and utilization. *Journal of Applied Botany-Angewandte Botanik* 71(5-6):189-194.

Two-week-old strawberry (*Fragaria x ananassa* Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO₂ in controlled environment chambers for 50 days. Raising CO₂ concentration from 300 to 900 ppm promoted macronutrient accumulation in all organs of the plants, particularly in roots. It, however, reduced contents of macronutrients in most organs of the plants, especially in leaves, because of the dilution effect of larger amounts of carbohydrate accumulation in the plant organs. When compared with the 300 ppm CO₂ treatment, 600 and 900 ppm CO₂ increased accumulation of N by 93 % and 87 %, P by 113 % and 122 %, K by 98 % and 92 %, Ca by 212 % and 244 %, and Mg by 177 % and 200 %, respectively. CO₂ enrichment decreased the proportions of N and K, increased those of Ca and Mg, but did not affect the proportion of P in the plants. Increasing CO₂ levels depressed macronutrient-uptake efficiency of the plant roots, but promoted macronutrient-use efficiency of the plants. In comparison with the 300 ppm CO₂-treated plants, those treated with 600 and 900 ppm CO₂ showed lower N-, P-, K-, Ca-, and Mg- uptake efficiency of the roots and higher N-, P-, K-, Ca-, and Mg- use efficiency of the plants.

KEYWORDS: ECOSYSTEMS, ELEVATED CO₂, ENRICHMENT, GROWTH, NITROGEN, PHOSPHORUS, RESPONSES, STRESS, TREES

380

Chen, K., G.Q. Hu, and F. Lenz. 1997. Effects of CO₂ concentration on strawberry. VI. Fruit yield and quality. *Journal of Applied Botany-*

Two-week-old strawberry (*Fragaria x ananassa* Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO₂ in controlled environment chambers for 50 and 60 days during vegetative growth in late autumn of 1995 and reproductive growth in early spring of 1996. High CO₂ promoted branch-crown and pedicel development as well as flower-bud differentiation. It also induced a second bloom. Flowering and fruit ripening started earlier and lasted for a longer period under high rather than low CO₂ concentrations. CO₂ enrichment shortened the periods of anthesis and single fruit growth but prolonged the periods of flowering and fruit harvest. Elevated CO₂ concentrations enhanced fruit productivity as indicated by increases in pedicel number per plant, fruit setting per pedicel, fruit size, and dry matter content of the fruits. In comparison with the 300 ppm CO₂ treatment, 450, 600, 750, and 900 ppm CO₂ increased average fruit yield per plant by 0.7, 2.7, 3.6, and 4.1 fold, daily growth per fresh fruit by 0.4, 1.0, 1.1, and 1.3 fold, and growth rate of fruit biomass per plant by 1.0, 3.9, 5.5, and 6.9 fold, respectively. High CO₂ tended to improve fruit quality as well. Raising CO₂ concentrations accelerated dry matter increment and total sugar accumulation in the fruits, especially for sucrose, and decreased titratable acid content, resulting in a higher sugar/acid ratio of the fruits. Contents of starch and minerals in the fruits slightly decreased when CO₂ rose.

KEYWORDS: ENRICHMENT

381

Chen, K., and F. Lenz. 1997. Responses of strawberry to doubled CO₂ concentration and phosphorus deficiency .1. Distribution of dry matter, macronutrients, and carbohydrates. *Gartenbauwissenschaft* 62(1):30-37.

One-year-old strawberry (*Fragaria x ananassa* Duch. cv. 'Elsanta') plants grown in controlled environmental chambers were supplied with a modified P-sufficient (0.5 mmol P l⁻¹) or P-deficient (0.05 mmol P l⁻¹) Hoagland nutrient solution and acclimatized by an ambient CO₂ (340 +/- 20 ppm) or doubled CO₂ (680 +/- 20 ppm) concentration for one month. Doubled CO₂ concentration promoted plant vegetative growth and dry matter assimilation, especially in leaf area enlargement, leaf dry weight, and runner extending growth. The plant responses to doubled CO₂ concentration were more pronounced under P-sufficient than P-deficient conditions. P deficiency not only moderated the above plant responses to CO₂ enrichment, but also accelerated premature leaf senescence and aggravated P-deficient symptoms at doubled CO₂ concentration. The mean increment in total dry matter of the plants in virtue of doubled CO₂ concentration and P-sufficiency were 25-63 % and 123-191 %, respectively. Doubled CO₂ concentration reduced N level in the plant organs, particularly in both new and old leaves and runners, while increased the contents of starch, glucose, fructose, sucrose, and total non-structural carbohydrates in most organs; but not particularly affected contents of P, K, Ca, and Mg. P deficiency decreased contents of N, P, K, Mg, and soluble carbohydrates, while increased root : shoot ratio and starch level in roots, stems, runners, and leaves whether at the ambient CO₂ or at doubled CO₂ condition. Neither doubled CO₂ nor P deficiency definitely altered Ca content in the plant organs.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, GROWTH, INCREASES, PLANTS, YIELD

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Chen, S.G., I. Impens, and R. Ceulemans. 1997. Modelling the effects of elevated atmospheric CO₂ on crown development, light interception and photosynthesis of poplar in open top chambers. *Global Change Biology* 3(2):97-106.

An open-top chamber experiment was carried out to examine the likely effects of elevated atmospheric [CO₂] on architectural as well as on physiological characteristics of two poplar clones (*Populus trichocarpa* x *P. deltoides* clone Beaupre and *P. deltoides* x *P. nigra* clone Robusta). Crown architectural parameters required as input parameters for a three-dimensional (3D) model of poplar structure, such as branching frequency and position, branch angle, internode length and its distribution pattern, leaf size and orientation, were measured following growth in ambient and elevated [CO₂] (ambient + 350 $\mu\text{mol mol}^{-1}$) treated open-top chambers. Based on this information, the light interception and photosynthesis of poplar canopies in different [CO₂] treatments were simulated using the 3D poplar tree model and a 3D radiative transfer model at various stages of the growing season. The first year experiments and modelling results showed that the [CO₂] enrichment had effects on light intercepting canopy structure as well as on leaf photosynthesis properties. The elevated [CO₂] treatment resulted in an increase of leaf area, canopy photosynthetic rate and above-ground biomass production of the two poplar clones studied. However, the structural components responded less than the process components to the [CO₂] enrichment. Among the structural components, the increase of LAI contributed the most to the canopy light interception and canopy photosynthesis; the change of other structural aspects as a whole caused by the [CO₂] enrichment had little effect on daily canopy light interception and photosynthesis.

KEYWORDS: CANOPYSTRUCTURE, CARBON DIOXIDE, FORESTS, GROWTH, PLANTS, POPULUS, SYSTEM

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Chen, S.G., I. Impens, and R. Ceulemans. 1997. Modelling the effects of elevated atmospheric CO₂ on crown development, light interception and photosynthesis of poplar in open top chambers (vol 3, pg 97, 1997). *Global Change Biology* 3(6):550.

384

Chen, X.M., G.B. Begonia, D.M. Alm, and J.D. Hesketh. 1993. Responses of soybean leaf photosynthesis to CO₂ and drought. *Photosynthetica* 29(3):447-454.

Soybean [*Glycine max* (L.) Merr. cv. Jack] was grown in the field in rain-protected plots to study effects of drought and atmospheric CO₂ enrichment, on leaf gas exchange. Midday depressions in leaf photosynthetic CO₂ exchange rates (P(N)) were found in drought-stressed plants and the diurnal changes were mostly stomatal-regulated, although accumulated drought stress eventually resulted in some non-stomatal limitations. However, seasonal changes in P(N) were mostly limited by non-stomatal factors. Water use efficiency was always higher for drought stressed plants and depended on the severity of stress and associated stomatal or nonstomatal limitations. At enriched atmospheric CO₂ levels, stomatal limitations to P(N) under drought stress were less important than at ambient atmospheric CO₂ levels. Morning and afternoon leaf starch levels were enhanced in both irrigated and nonirrigated plants in enriched CO₂. Afternoon starch levels were higher in stressed leaves than in non-stressed leaves at normal CO₂ levels.

KEYWORDS: AIR, EXPOSURE, RATES, STRESS, WATER DEFICIT

385

Chen, X.M., G.B. Begonia, and J.D. Hesketh. 1995. Soybean stomatal acclimation to long-term exposure to CO₂-enriched atmospheres. *Photosynthetica* 31(1):51-57.

Soybean [*Glycine max* (L.) cv. Jack] grown in open top chambers under controlled laboratory and field conditions was used to study the

acclimation of leaf gas exchange processes to CO₂ enrichment. Air inside the open top chambers was maintained at either 700-800 or 350-400 $\mu\text{mol}(\text{CO}_2)\text{mol}^{-1}(\text{air})$. Leaf gas exchange rates were measured for some plants switched between treatments. When measured in the CO₂-enriched atmosphere, stomatal conductances ($g(s)$) were higher in leaves grown in CO₂-enriched atmospheres than in those grown under ambient conditions, and the lower $g(s)$ values for plants in the CO₂-enriched atmospheres were limiting to leaf net photosynthetic CO₂ exchange rates (P-N). P-N of enriched leaves was higher than those of the ambient controls when measured at elevated CO₂ levels in both controlled environment and field studies, while it was depressed in enriched leaves when measured under ambient CO₂ conditions, and this drop in P-N did not recover until 6-15 d after plants were placed back in ambient conditions.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, PHOTOSYNTHETIC INHIBITION

386

Chenevard, D., C. Jayallemand, M. Gendraud, and J.S. Frossard. 1995. The effect of sucrose on the development of hybrid walnut microcuttings (*Juglans-nigra* X *Juglans-regia*) - consequences on their survival during acclimatization. *Annales Des Sciences Forestieres* 52(2):147-156.

We studied the effect of sucrose concentration in the root- development medium on the formation of adventitious roots and survival of microcuttings during acclimatization in 2 interspecific hybrid walnut (*Juglans nigra* n degrees 23 x *J regia*) clones. Sucrose increased the rooting percentage (fig 1), the number of adventitious roots (fig 2A) and the dry- matter content (table I) per rooted shoot. These effects were due to the energy properties of sucrose rather than to its osmotic function. High sucrose concentrations in the root- development medium (> 20 $g.l^{-1}$) resulted in a high soluble carbohydrate content in the plantlets (fig 3), mainly located in roots and callus. The 2-clones showed different capacities in rooting and growth. Survival of microcuttings during acclimatization was not directly influenced by the sucrose concentration (fig 5) but was correlated with the number of adventitious roots (fig 6A) as well as with the number of leaves (fig 6B) present at the time of transfer to the growth chamber for each individual plant.

KEYWORDS: ACCUMULATION, CO₂- ENRICHMENT, CULTURE, GROWTH, INVITRO, PLANTS, PROPAGATION, SHOOT, TEMPERATURE

387

Cheng, S.H., B.D. Moore, and J.R. Seemann. 1998. Effects of short- and long-term elevated CO₂ on the expression of ribulose-1,5-bisphosphate carboxylase/oxygenase genes and carbohydrate accumulation in leaves of *Arabidopsis thaliana* (L) Heynh. *Plant Physiology* 116(2):715-723.

To investigate the proposed molecular characteristics of sugar- mediated repression of photosynthetic genes during plant acclimation to elevated CO₂, we examined the relationship between the accumulation and metabolism of nonstructural carbohydrates and changes in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) gene expression in leaves of *Arabidopsis thaliana* exposed to elevated CO₂. Long-term growth of *Arabidopsis* at high CO₂ (1000 $\mu\text{mol L}^{-1}$) resulted in a 2-fold increase in nonstructural carbohydrates, a large decrease in the expression of Rubisco protein and in the transcript of *rbcL*, the gene encoding the large subunit of Rubisco (approximately 35-40%), and an even greater decline in mRNA of *rbcS*, the gene encoding the small subunit (approximately 60%). This differential response of protein and mRNAs suggests that transcriptional/posttranscriptional processes and protein turnover may determine the final amount of leaf Rubisco protein at high

CO₂. Analysis of mRNA levels of individual *rbcS* genes indicated that reduction in total *rbcS* transcripts was caused by decreased expression of all four *rbcS* genes. Short-term transfer of *Arabidopsis* plants grown at ambient CO₂ to high CO₂ resulted in a decrease in total *rbcS* mRNA by d 6, whereas Rubisco content and *rbcL* mRNA decreased by d 9. Transfer to high CO₂ reduced the maximum expression level of the primary *rbcS* genes (1A and, particularly, 3B) by limiting their normal pattern of accumulation through the night period. The decreased nighttime levels of *rbcS* mRNA were associated with a nocturnal increase in leaf hexoses. We suggest that prolonged nighttime hexose metabolism resulting from exposure to elevated CO₂ affects *rbcS* transcript accumulation and, ultimately, the level of Rubisco protein.

KEYWORDS: CARBON METABOLISM, LEAF DEVELOPMENT, MESSENGER-RNA, METABOLIC REPRESSION, PHOTOSYNTHESIS, RBCS GENES, SMALL-SUBUNIT, TOMATO PLANTS, TRANSGENIC TOBACCO PLANTS, YEAST- DERIVED INVERTASE

388

Cheng, W.X. 1999. Rhizosphere feedbacks in elevated CO₂. *Tree Physiology* 19(4-5):313-320.

Understanding rhizosphere processes in relation to increasing atmospheric CO₂ concentrations is important for predicting the response of forest ecosystems to environmental changes, because rhizosphere processes are intimately linked with nutrient cycling and soil organic matter decomposition, both of which feedback to tree growth and soil carbon storage. Plants grown in elevated CO₂ substantially increase C input to the rhizosphere. Although it is known that elevated CO₂ enhances rhizosphere respiration more than it enhances root biomass, the fate and function of this extra carbon input to the rhizosphere in response to elevated CO₂ are not clear. Depending on specific plant and soil conditions, the increased carbon input to the rhizosphere can result in an increase, a decrease, or no effect on soil organic matter decomposition and nutrient mineralization. Three mechanisms may account for these inconsistent results: (1) the "preferential substrate utilization" hypothesis; (2) the "priming effect" hypothesis; and (3) the "competition" hypothesis, i.e., competition for mineral nutrients between plants and soil microorganisms. A microbial growth model is developed that quantitatively links the increased rhizosphere input in response to elevated CO₂ with soil organic matter decomposition. The model incorporates the three proposed mechanisms, and simulates the complexity of the rhizosphere processes. The model also illustrates mechanistically the interactions among nitrogen availability, substrate quality, and microbial dynamics when the system is exposed to elevated CO₂.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, LONG-TERM, MICROBIAL BIOMASS, MYCORRHIZAL COLONIZATION, NITROGENASE ACTIVITY, PINE SEEDLINGS, PISUM-SATIVUM, QUERCUS-ALBA, SOIL ORGANIC MATTER

389

Cheng, W.X., and D.W. Johnson. 1998. Elevated CO₂, rhizosphere processes, and soil organic matter decomposition. *Plant and Soil* 202(2):167-174.

The rhizosphere is one of the key fine-scale components of C cycles. This study was undertaken to improve understanding of the potential effects of atmospheric CO₂ increase on rhizosphere processes. Using C isotope techniques, we found that elevated atmospheric CO₂ significantly increased wheat plant growth, dry mass accumulation, rhizosphere respiration, and soluble C concentrations in the rhizosphere. When plants were grown under elevated CO₂ concentration, soluble C concentration in the rhizosphere increased by approximately 60%. The degree of elevated CO₂ enhancement on rhizosphere respiration was

much higher than on root biomass. Averaged between the two nitrogen treatments and compared with the ambient CO₂ treatment, wheat rhizosphere respiration rate increased 60% and root biomass only increased 26% under the elevated CO₂ treatment. These results indicated that elevated atmospheric CO₂ in a wheat-soil system significantly increased substrate input to the rhizosphere due to both increased root growth and increased root activities per unit of roots. Nitrogen treatments changed the effect of elevated CO₂ on soil organic matter decomposition. Elevated CO₂ increased soil organic matter decomposition (22%) in the nitrogen-added treatment but decreased soil organic matter decomposition (18%) without nitrogen addition. Soil nitrogen status was therefore found to be important in determining the directions of the effect of elevated CO₂ on soil organic matter decomposition.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ENRICHMENT, GLOBAL CHANGE, GROWTH, NITROGENASE ACTIVITY, PINE SEEDLINGS, PISUM-SATIVUM, RESPONSES, SYSTEM

390

Kryukov, T., J.M. Robinson, E.H. Lee, and C.L. Mulchi. 1997. Evaluation of ozone tolerance mechanisms in soybean cultivars exposed to ambient and elevated CO₂. *Plant Physiology* 114(3):201.

391

Chmora, S.N., and A.T. Mokronosov. 1994. The global increase of CO₂ in the atmosphere - adaptive strategies in plants. *Russian Journal of Plant Physiology* 41(5):677-685.

The effects of short- and long-term exposure to increased CO₂ concentrations on the life activity and productivity of plants are discussed. Two strategies of plant adaptation to an increasing CO₂ concentration are outlined that reflect the diversity of adaptive plant responses at the ecological and physiological levels: physiological adaptation that occurs at all organization levels from molecular to genetic and changes in areas of species that lead to changes in ecosystem composition occurring in correspondence to the biochemical diversity of photosynthetic pathways.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO₂, ENRICHMENT, GROWTH, PHOTOSYNTHESIS, WHEAT, YIELD

392

Chomba, B.M., R.D. Guy, and H.G. Weger. 1993. Carbohydrate reserve accumulation and depletion in Engelmann spruce (*Picea engelmannii* Parry) - effects of cold-storage and prestorage CO₂ enrichment. *Tree Physiology* 13(4):351-364.

The effects of pre-storage CO₂ enrichment on growth, non-structural carbohydrates and post-storage root growth potential of Engelmann spruce (*Picea engelmannii* Parry) seedlings were studied. Seedlings were grown from seed for 202 days in growth chambers with ambient (340 µmol l⁻¹) or CO₂-enriched (1000 µmol l⁻¹) air. Some seedlings were transferred between CO₂ treatments at 60 and 120 days. Photoperiod was reduced at 100 days to induce bud set and temperature was reduced at 180 days to promote frost hardiness development for storage at -5 degrees C for 2 or 4 months. Stored seedlings were planted in a growth chamber after thawing for one week at +5 degrees C. At 80, 120, 140 and 202 days, and at each planting time after storage, seedlings were harvested for growth measurements and analysis of starch and soluble sugar concentrations. Planted seedlings were assessed for bud break every two days and new roots > 5 mm long were counted after four weeks. Carbon dioxide enrichment increased root collar diameter and

almost doubled seedling biomass, with the most obvious effects occurring after bud set. Stem height was affected only slightly and shoot/root ratios were not affected at all. Carbon dioxide enrichment increased the rate of reserve carbohydrate accumulation, but did not influence the final concentration attained before storage (accounting for 32% of seedling dry weight). Needles were the major storage organ for soluble sugars, whereas roots were the major storage organ for starch. Soluble sugars were not strongly affected by two or four months of storage, but starch was reduced by more than 50% in all plant parts. None of the CO₂ treatments had an impact on bud break or root growth potential.

393

Christ, R.A., and C. Korner. 1995. Responses of shoot and root gas-exchange, leaf blade expansion and biomass production to pulses of elevated CO₂ in hydroponic wheat. *Journal of Experimental Botany* 46(292):1661-1667.

Short-term effects of elevated CO₂ during the early life phase of plants may have long lasting consequences for growth and biomass in later periods. We exposed hydroponically grown wheat seedlings to 5 d pulses of elevated CO₂ while leaf expansion growth as well as shoot and root gas exchange were measured simultaneously and continuously. Shoot photosynthesis, night-time shoot respiration and below-ground respiration (largely by roots) roughly doubled when atmospheric CO₂ concentration was doubled. An interruption of CO₂ enrichment caused CO₂ assimilation and respiration to return to control levels. However, while the response of photosynthesis was immediate, that of respiration showed a hysteresis of about 3 d. Since shoot biomass increased at elevated CO₂ (with no change in allocation pattern) equal fluxes per shoot or root system after a return to control CO₂ concentrations indicate substantial downward adjustment of the capacity for CO₂ fixation and release in high-CO₂ grown plants. Leaf expansion growth was completely unaffected by CO₂ enrichment, whereas tiller initiation was significantly increased (doubled in 18 d). We conclude that leaf growth in these wheat plants was already carbon-saturated at ambient CO₂ concentration at optimum mineral nutrient supply. The stimulation of growth of whole plants was exclusively due to enhanced tillering during this very early part of the life of these wheat plants.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, EXTENSION, FIELD, GROWTH, LEAVES, PLANTS, RESPIRATION, TEMPERATURE, WINTER-WHEAT, YIELD

394

Christensen, T.R., S. Jonasson, T.V. Callaghan, and M. Havstrom. 1999. On the potential CO₂ release from tundra soils in a changing climate. *Applied Soil Ecology* 11(2-3):127-134.

About 30% of the carbon in terrestrial ecosystems is stored in northern wetlands and boreal forest regions. Prevailing cold and wet soil conditions have largely been responsible for this carbon accumulation. It has been suggested that a warmer and drier climate in these regions might increase the decomposition rate and, hence, release more CO₂ to the atmosphere than at present. This study reports on the spatial variability and temperature dependence of the potential carbon release after incubating highly organic soils from the European Arctic and Siberia at different temperatures. We found that the decay potential, measured as CO₂ production in laboratory experiments, differed strongly within and among sites, particularly at higher soil temperatures. Furthermore, both the decay potential and its temperature response decreased significantly with depth in the soil, presumably because the older soils at deeper layers contained higher proportions of recalcitrant carbon than the younger soil organic matter at the surface. These results have implications for global models of potential feedbacks on climate

change inferred from changes in the carbon balance of northern wetlands and tundra. Firstly, because the decay potential of the organic matter varies locally as well as regionally, predictions of how the tundra carbon balance may change will be unreliable if these are based on measurements at a few sites only. Secondly, any increase in CO₂ production may be transitional as both the carbon flux and its temperature sensitivity decrease when the most easily degradable organic material near the soil surface has decomposed. Consequently, it is crucial to account for transient responses and regional differences in the models of potential feedbacks on climate change from changed carbon cycling in northern terrestrial ecosystems. (C) 1999 Elsevier Science B.V.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, FLUX, SINK

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Christensen, T.R., S. Jonasson, T.V. Callaghan, M. Havstrom, and F.R. Livens. 1999. Carbon cycling and methane exchange in Eurasian tundra ecosystems. *Ambio* 28(3):239-244.

This paper provides an overview of data and results obtained through a number of studies of actual and potential trace gas exchanges in northern Eurasia, made possible through the Swedish-Russian Tundra Ecology - 94 expedition. It was found that: i) long-term accumulation rates of carbon in organic tundra soils, i.e. net uptake of atmospheric CO₂, correlated with simple climatic parameters, such as mean July temperature and annual precipitation; ii) the release of carbon through ecosystem respiration is also strongly controlled by climate. Increased temperature and decrease of water-logging enhanced the CO₂ flux. However, the release of organic soil carbon as CO₂ is also constrained by other factors such as poor decomposability of the stored organic compounds; and iii) methane emissions from typical tundra habitats in northern Eurasia were found to be slightly lower than from seemingly similar habitats in North America. This difference can probably be attributed to lower temperatures along the Russian arctic coast than at North American sites in general.

KEYWORDS: DIOXIDE, EMISSION

396

Chu, C.C., J.S. Coleman, and H.A. Mooney. 1992. Controls of biomass partitioning between roots and shoots - atmospheric CO₂ enrichment and the acquisition and allocation of carbon and nitrogen in wild radish. *Oecologia* 89(4):580-587.

The effects of CO₂ enrichment on plant growth, carbon and nitrogen acquisition and resource allocation were investigated in order to examine several hypotheses about the mechanisms that govern dry matter partitioning between shoots and roots. Wild radish plants (*Raphanus sativus* x *raphanistrum*) were grown for 25 d under three different atmospheric CO₂ concentrations (200 ppm, 330 ppm and 600 ppm) with a stable hydroponic 150- μ mol l⁻¹ nitrate supply. Radish biomass accumulation, photosynthetic rate, water use efficiency, nitrogen per unit leaf area, and starch and soluble sugar levels in leaves increased with increasing atmospheric CO₂ concentration, whereas specific leaf area and nitrogen concentration of leaves significantly decreased. Despite substantial changes in radish growth, resource acquisition and resource partitioning, the rate at which leaves accumulated starch over the course of the light period and the partitioning of biomass between roots and shoots were not affected by CO₂ treatment. This phenomenon was consistent with the hypothesis that root/shoot partitioning is related to the daily rate of starch accumulation by leaves during the photoperiod, but is inconsistent with hypotheses suggesting that root/shoot partitioning is controlled by some aspect of plant C/N balance.

KEYWORDS: CARROT, COMPETITION, DIOXIDE, ELEVATED CO₂, MODEL, NITRATE, PLANT GROWTH, PROGRAM, RESPONSES, TOMATO

397

Chu, C.C., C.B. Field, and H.A. Mooney. 1996. Effects of CO₂ and nutrient enrichment on tissue quality of two California annuals. *Oecologia* 107(4):433-440.

The effects of CO₂ enrichment and soil nutrient status on tissue quality were investigated and related to the potential effect on growth and decomposition. Two California annuals, *Avena fatua* and *Plantago erecta*, were grown at ambient and ambient plus 35 Pa atmospheric CO₂ in nutrient unamended and amended serpentine soil. Elevated CO₂ led to significantly increased *Avena* shoot nitrogen concentrations in the nutrient amended treatment. It also led to decreased lignin concentrations in *Avena* roots in both nutrient treatments, and in *Plantago* shoots and roots with nutrient addition. Concentrations of total nonstructural carbohydrate (TNC) and carbon did not change with elevated CO₂ in either species. As a consequence of increased biomass accumulation, increased CO₂ led to larger total pools of TNC, lignin, total carbon, and total nitrogen in *Avena* with nutrient additions. Doubling CO₂ had no significant effect on *Plantago*. Given the limited changes in the compounds related to decomposability and plant growth, effects of increased atmospheric CO₂ mediated through tissue composition on *Avena* and *Plantago* are likely to be minor and depend on site fertility. This study suggests that other factors such as litter moisture, whether or not litter is on the ground, and biomass allocation among roots and shoots, are likely to be more important in this California grassland ecosystem. CO₂ could influence those directly as well as indirectly.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, ELEVATED CO₂, LIGNIN CONTROL, LITTER DECOMPOSITION, LONG-TERM DECOMPOSITION, NITROGEN, PLANTS, RESPONSES, SCOTS PINE FOREST

398

Ciais, P., P. Friedlingstein, D.S. Schimel, and P.P. Tans. 1999. A global calculation of the delta C-13 of soil respired carbon: Implications for the biospheric uptake of anthropogenic CO₂. *Global Biogeochemical Cycles* 13(2):519-530.

The continuing emissions of fossil CO₂ depleted in C-13 have been causing a gradual decrease in atmospheric delta(13)C by roughly 1.4 parts per thousand since preindustrial times. The progressive penetration of this perturbation into the land biota causes the soil organic matter to be enriched in 13C with respect to recently formed plant material. This effect which we call the "biotic isotope disequilibrium" is important when it comes to deducing the terrestrial carbon fluxes by using delta(13)C in atmospheric CO₂. We have estimated the geographical distribution of the isotopic disequilibrium, which is primarily influenced by the turnover of carbon in the various ecosystems, from the output of two biospheric models, (SLAVE and CENTURY). The disequilibrium is estimated to shift up the delta(13)C of atmospheric CO₂ by the same amount as a net sink of 0.6 Gt C yr⁻¹ in the land biota. This "fake" terrestrial sink due to the isotopic disequilibrium is distributed mainly in northern midlatitudes (0.2 Gt C yr⁻¹) and tropical forests (0.3 Gt C yr⁻¹).

KEYWORDS: ATMOSPHERIC CO₂, ISOTOPE, SIMULATION, TURNOVER, WORLDWIDE

399

Cipollini, M.L., B.G. Drake, and D. Whigham. 1993. Effects of

elevated CO₂ on growth and carbon/nutrient balance in the deciduous woody shrub *Lindera benzoin* (L.) Blume (Lauraceae). *Oecologia* 96(3):339-346.

We examined the effects of elevated CO₂ on growth and carbon/nutrient balance in a natural population of the deciduous temperate zone shrub *Lindera benzoin*. Our data concern whole plant, leaf, and stem growth for the first two seasons of a long-term field experiment in which CO₂ levels were manipulated in situ. In addition to growth parameters, we evaluated changes in leaf and stem chemistry, including total nitrogen, nonstructural carbohydrates, and total phenolics. Over the course of this study, *L. benzoin* appeared to respond to elevated CO₂ primarily by physiological and biochemical changes, with only a slight enhancement in aboveground growth (ramet height). Positive effects on aboveground growth were primarily evident in young (nonreproductive) ramets. Our results suggest that nitrogen limitation may have constrained plants to allocate carbohydrates produced in response to elevated CO₂ primarily to storage and belowground growth, and perhaps to increased secondary chemical production, rather than to increased stem and leaf growth. We discuss our results in terms of changes in carbon/nutrient balance induced by elevated CO₂, and provide predictions for future changes in this system based upon constraints imposed by intrinsic and extrinsic factors and their potential effects on the reallocation of stored reserves.

KEYWORDS: ATMOSPHERIC CO₂, AVAILABILITY, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, FOREST, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES, TREES

400

Clark, D.G., J.W. Kelly, and N.C. Rajapakse. 1993. Production and postharvest characteristics of rosa-hybrida *L. meijikatar* grown in pots under carbon-dioxide enrichment. *Journal of the American Society for Horticultural Science* 118(5):613-617.

The effects of carbon dioxide enrichment on growth, photosynthesis, and postharvest characteristics of 'Meijikatar' potted roses were determined. Plants were grown in 350, 700, or 1050 µmol CO₂/liter until they reached 50% flower bud coloration and then were placed into dark storage for 5 days at 4 or 16°C. Plants grown in 700 or 1050 µmol CO₂/liter reached the harvest stage earlier and were taller at harvest than plants produced in 350 µmol CO₂/liter, but there were no differences in the number of flowers and flower buds per plant among CO₂ treatments. Plants grown in early spring were taller and had more flowers and flower buds than plants grown in late winter. Shoot and root growth of plants grown in 700 or 1050 µmol CO₂/liter were higher than in plants produced in 350 µmol CO₂/liter, with plants grown in early spring showing greater increases than plants grown in late winter. Immediately after storage, plants grown in 350 µmol CO₂/liter and stored at 4°C had the fewest etiolated shoots, while plants grown in 1050 µmol CO₂/liter and stored at 16°C had the most. Five days after removal from storage, chlorophyll concentration of upper and lower leaves had been reduced by almost-equal-to 50% from the day of harvest. Carbon dioxide enrichment had no effect on postharvest leaf chlorosis, but plants grown in early spring and stored at 16°C had the most leaf chlorosis while plants grown in late winter and stored at 4°C had the least leaf chlorosis.

KEYWORDS: CO₂- ENRICHMENT, ENVIRONMENT, LIGHT, MORIFOLIUM RAMAT, N,N-DIMETHYLFORMAMIDE, PLANTS, RESPONSES

401

Clark, H., P.C.D. Newton, and D.J. Barker. 1999. Physiological and morphological responses to elevated CO₂ and a soil moisture deficit of temperate pasture species growing in an established plant community. *Journal of Experimental Botany* 50(331):233-242.

Periods of limited soil water availability are a feature of many temperate pasture systems and these have the potential to modify pasture plant and community responses to elevated atmospheric CO₂. Using large pasture turves, previously exposed to elevated CO₂ concentrations of 350 or 700 µmol mol⁻¹ for 324 d under well-watered conditions, the morphological and physiological responses of pasture species growing at these CO₂ concentrations were compared when subjected to a soil moisture deficit-and to recovery from the deficit-with those that continued to be well watered. Net leaf photosynthesis of *Trifolium repens* (C-3 legume), *Plantago lanceolata* (C-3) and *Paspalum dilatatum* (C-4) was increased by exposure to elevated CO₂, but there was no consistent effect of CO₂ on stomatal conductance. At low soil moistures, net photosynthesis declined and stomatal conductance increased in these three species. There was a strong CO₂ x water interaction in respect of net photosynthesis; in *Trifolium repens*, for example, elevated CO₂ increased net photosynthesis by approximately 50% under well-watered conditions and this increased to over 300% when soil moisture levels reached their minimum values. Similar values were recorded for both *Paspalum dilatatum* and *Plantago lanceolata*. Potential water use efficiency (net photosynthesis/stomatal conductance) was increased by both exposure to elevated CO₂ and drought. Leaf water status was measured in three species: *Trifolium repens*, *Paspalum dilatatum* and *Holcus lanatus* (C-3). Total leaf water potential (psi(t)) and osmotic potential (psi(pi)) were decreased by drought, but CO₂ concentration had no consistent effect. psi(t) and psi(pi) were highest in the C-4 species *Paspalum dilatatum* and lowest in the legume *Trifolium repens*. In the wet turves, rates of leaf extension of the C-3 grasses *Holcus lanatus* and *Lolium perenne* at elevated CO₂ were frequently higher than those at ambient CO₂, but there was no effect of CO₂ concentration on the rate recorded in the C-4 grass *Paspalum dilatatum* or the rate of leaf appearance in the legume *Trifolium repens*. Drought reduced leaf extension rate irrespective of CO₂ in all species, but in *Holcus lanatus* the reduction was less severe at elevated CO₂. Immediately after the dry turves were rewatered the leaf extension rates on tillers of *Holcus lanatus* and *Lolium perenne* were higher than on tillers in the wet turves, but only at ambient CO₂. Consequently, despite the greater leaf extension rate during the soil moisture deficit at elevated CO₂, because of the overcompensation after rewatering at ambient CO₂, total leaf extension over both the drying and rewetting period did not differ between CO₂ concentrations for these C-3 grass species. Further investigation of this difference in response between CO₂ treatments is warranted given the frequent drying and wetting cycles experienced by many temperate grasslands.

KEYWORDS: BIOMASS PRODUCTION, C-4 GRASS, CARBON-DIOXIDE CONCENTRATIONS, GAS-EXCHANGE, LOLIUM-PERENNE, SIMULATED SEASONAL-CHANGES, STOMATAL RESPONSES, TRIFOLIUM-REPENS, WATER-USE, WHITE CLOVER

402

Clark, H., P.C.D. Newton, C.C. Bell, and E.M. Glasgow. 1995. The influence of elevated CO₂ and simulated seasonal-changes in temperature on tissue turnover in pasture turves dominated by perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*). *Journal of Applied Ecology* 32(1):128-136.

1. Tissue turnover, leaf morphology and population dynamics of perennial ryegrass and white clover were studied in pasture turves grown at ambient (350 µmol mol⁻¹) or double ambient (700 µmol mol⁻¹) CO₂ concentrations for 217 days in controlled environment rooms. The turves were subjected sequentially to three day/night temperature regimes; 10/4 degrees C, 16/10 degrees C and 22/16 degrees C and harvested at 3-week intervals. The photoperiod was 12 hours for all of the temperature treatments with a mean photon flux density of 480 µmol m⁻² s⁻¹. 2. Ryegrass leaf extension and leaf death rates did not differ between CO₂ treatments and there was no effect of CO₂ on rates of leaf appearance in white clover. Weight per unit length of ryegrass

laminae was unaffected by elevated CO₂ but lamina weight per unit area, lamina area and petiole weight per unit length in white clover showed a small positive response, especially at the two higher temperatures. Rates of growth and senescence per ryegrass tiller were therefore similar between CO₂ treatments, but rates of growth per white clover growing point were increased by 4, 23 and 13% at 10/4 degrees C, 16/10 degrees C and 22/16 degrees C, respectively, at elevated CO₂. Responses to CO₂ could not be attributed to any consistent change in morphological characteristics in either species and exposure to elevated concentrations of CO₂ did not appear to change the relationship between growth and senescence per meristem. 3. Total grass tiller populations were similar at both CO₂ concentrations, but ryegrass tiller densities more than halved in both CO₂ treatments as the temperature was increased. The fall was most severe at 700 μmol mol⁻¹ and at the end of the experiment ryegrass tiller densities in this treatment were only 47% of those found at 350 μmol mol⁻¹. There was no consistent effect of CO₂ concentration on clover growing point numbers and they increased from 800 m⁻² to over 3000 m⁻² in both treatments with maximum densities occurring at 22/16 degrees C. 4. The results imply that, in plant communities dominated by ryegrass and white clover, exposure to elevated CO₂ concentrations will alter the species composition in favour of white clover. Responses in above-ground dry matter yield to elevated CO₂ will be a balance between the positive response shown by white clover and the negative response of perennial ryegrass. Temperature will have a major influence on the magnitude of this response since both the response of white clover to CO₂ and the ratio of white clover growing points to ryegrass tillers are temperature-dependent.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, COMMUNITIES, DEATH, LEAF, PHOTOSYNTHESIS, REPRODUCTIVE GROWTH, SENESCENCE, SWARDS, TILLER

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Clark, H., P.C.D. Newton, C.C. Bell, and E.M. Glasgow. 1997. Dry matter yield, leaf growth and population dynamics in *Lolium perenne* *Trifolium repens*-dominated pasture turves exposed to two levels of elevated CO₂. *Journal of Applied Ecology* 34(2):304-316.

1. Dry matter yield, leaf growth and population dynamics of turves taken from an old *Lolium perenne*/*Trifolium repens*-dominated pasture were studied in controlled environment rooms at CO₂ concentrations of 350 μmol mol⁻¹, 525 μmol mol⁻¹ and 700 μmol mol⁻¹. Starting with September data the turves were subjected sequentially to the mean monthly temperature and photoperiod taken from long-term climatic data for the area of New Zealand where the pasture was located. Each temperature and photoperiod regime was applied for 21 days to provide 12 different simulated 'months' of environmental conditions. The experiment ran for 14 simulated months, with September and October conditions being repeated at the end of the first simulated 'year'. Mean photon flux density throughout was 500 μmol m⁻² s⁻¹. 2. The total quantity of herbage harvested was increased by 7% and 14% at 525 μmol mol⁻¹ and 700 μmol mol⁻¹ CO₂, respectively. The increase in the amount of *T. repens* harvested by the end of the experiment was 63% at 525 μmol mol⁻¹ CO₂ and 48% at 700 μmol mol⁻¹ CO₂. In contrast, neither the yield of C3 grasses nor the yield of the only C4 grass present, *Paspalum dilatatum*, was significantly affected by CO₂ concentration. The implications of this increase in the proportion of *T. repens* in temperate pastures at elevated CO₂ is discussed briefly. 3. With the exception of a small increase in the specific leaf area of *T. repens*, detailed measurements of leaf growth on marked tillers (*L. perenne* and *P. dilatatum*) and growing points (*T. repens*) showed no consistent effects of exposure to elevated CO₂ concentrations. 4. Differences in yield between CO₂ concentrations were mainly attributable to changes in the number and balance of population units. By the middle of the 'winter' conditions *T. repens* growing point densities at 700 μmol mol⁻¹ CO₂ were more than double those

found at 350 μmol mol⁻¹ but total grass tiller densities were unchanged. Growing point densities were also more than doubled at 525 μmol mol⁻¹ CO₂ compared with 350 μmol mol⁻¹ but grass tiller densities were reduced significantly below those recorded in the other two treatments. The relationship between the stability of herbage production and population densities is discussed and the potential interaction between population density, elevated CO₂ and grazing considered. 5. Although exposure to elevated levels of CO₂ did result in large changes in population numbers, this did not happen immediately and so the yield response of this particular community to CO₂ varied with time. The average yield increases recorded here at elevated CO₂ may therefore tend to underestimate those likely to be shown by communities that, at the population level, have become fully adapted to growth in a CO₂-enriched atmosphere.

KEYWORDS: BIOMASS PRODUCTION, CARBON DIOXIDE, ENRICHMENT, INCREASING CO₂, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, SIMULATED SEASONAL-CHANGES, TEMPERATURE, WHITE CLOVER

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Clausen, M., and M. Esch. 1994. Biomes computed from simulated climatologies. *Climate Dynamics* 9(4-5):235-243.

The biome model of Prentice et al. (1992a) is used to predict global patterns of potential natural plant formations, or biomes, from climatologies simulated by ECHAM, a model used for climate simulations at the Max-Planck-Institut für Meteorologie. This study is undertaken in order to show the advantage of this biome model in diagnosing the performance of a climate model and assessing effects of past and future climate changes predicted by a climate model. Good overall agreement is found between global patterns of biomes computed from observed and simulated data of present climate. But there are also major discrepancies indicated by a difference in biomes in Australia, in the Kalahari Desert, and in the Middle West of North America. These discrepancies can be traced back to failures in simulated rainfall as well as summer or winter temperatures. Global patterns of biomes computed from an ice age simulation reveal that North America, Europe, and Siberia should have been covered largely by tundra and taiga, whereas only small differences are seen for the tropical rain forests. A potential northeast shift of biomes is expected from a simulation with enhanced CO₂ concentration according to the IPCC Scenario A. Little change is seen in the tropical rain forest and the Sahara. Since the biome model used is not capable of predicting changes in vegetation patterns due to a rapid climate change, the latter simulation has to be taken as a prediction of changes in conditions favourable for the existence of certain biomes, not as a prediction of a future distribution of biomes.

KEYWORDS: ATMOSPHERE, MODEL

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Clifford, S.C., C.R. Black, J.A. Roberts, I.M. Stronach, P.R. Singleton-Jones, A.D. Mohamed, and S.N. Azamali. 1995. The effect of elevated atmospheric CO₂ and drought on stomatal frequency in groundnut (*Arachis hypogaea* (L)). *Journal of Experimental Botany* 46(288):847-852.

The effects of elevated atmospheric CO₂, alone or in combination with water stress, on stomatal frequency in groundnut (*Arachis hypogaea* (L.) cv. Kadiri-3) were investigated. CO₂ exerted significant effects on stomatal frequency only in irrigated plants. The effects of drought on leaf development outweighed the smaller effects of CO₂ concentration, although reductions in stomatal frequency induced by elevated atmospheric CO₂ were still observed. When stands of groundnut were grown under irrigated conditions with unrestricted root systems, an increase in atmospheric CO₂ from 375 to 700 ppmv decreased stomatal

frequency on both leaf surfaces by up to 16%; in droughted plants, stomatal frequency was reduced by 8% on the adaxial leaf surface only. Elevated atmospheric CO₂ promoted larger reductions in leaf conductance than the changes in stomatal frequency, indicating partial stomatal closure. As a result, the groundnut stands grown at elevated CO₂ utilized the available soil moisture more slowly than those grown under ambient CO₂, thereby extending the growing period. Despite the large variations in cell frequencies induced by drought, there was no treatment effect on either stomatal index or the adaxial/abaxial stomatal frequency ratio. The data suggest that the effects of future increases in atmospheric CO₂ concentration on stomatal frequency in groundnut are likely to be small, especially under conditions of water stress, but that the combination of associated reductions in leaf conductance and enhanced assimilation at elevated CO₂ will be important in semi-arid regions.

KEYWORDS: DENSITY, ENRICHMENT, INCREASE, RESPONSES

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Clifford, S.C., I.M. Stronach, A.D. Mohamed, S.N. Azamali, and N.M.J. Crout. 1993. The effects of elevated atmospheric carbon-dioxide and water- stress on light interception, dry-matter production and yield in stands of groundnut (*arachis-hypogaea* L.). *Journal of Experimental Botany* 44(269):1763-1770.

Stands of groundnut (*Arachis hypogaea* L.), a C-3 legume, were grown in controlled-environment glasshouses at 28 degrees C (15 degrees C) under two levels of atmospheric CO₂ (350 ppmv or 700 ppmv) and two levels of soil moisture (irrigated weekly or no water from 35 d after sowing). Elevated CO₂ increased the maximum rate of net photosynthesis by up to 40%, with an increase in conversion coefficient for intercepted radiation of 30% (from 1.66 to 2.16 g MJ(-1)) in well-irrigated conditions, and 94% (from 0.64 to 1.24 g MJ(-1)) on a drying soil profile. In plants well supplied with water, elevated CO₂ increased dry matter accumulation by 16% (from 13.79 to 16.03 t ha(-1)) and pod yield by 25% (from 2.7 to 3.4 t ha(-1)). However, the harvest index (total pod dry weight/above-ground dry weight) was unaffected by CO₂ treatment. The beneficial effects of elevated CO₂ were enhanced under severe water stress, dry matter production increased by 112% (from 4.13 to 8.87 t ha(-1)) and a pod yield of 1.34 t ha(-1) was obtained in elevated CO₂, whereas comparable plots at 350 ppmv CO₂ only yielded 0.22 t ha(-1). There was a corresponding decrease in harvest index from 0.15 to 0.05. Following the withholding of irrigation, plants growing on a stored soil water profile in elevated CO₂ could maintain significantly less negative leaf water potentials (P<0.01) for the remainder of the season than comparable plants grown in ambient CO₂, allowing prolonged plant activity during drought. In plants which were well supplied with water, allocation of dry matter between leaves, stems, roots, and pods was similar in both CO₂ treatments. On a drying soil profile, allocation in plants grown in 350 ppmv CO₂ changed in favour of root development far earlier in the season than plants grown at 700 ppmv CO₂, indicating that severe water stress was reached earlier at 350 ppmv CO₂. The primary effects of elevated CO₂ on growth and yield of groundnut stands were mediated by an increase in the conversion coefficient for intercepted radiation and the prolonged maintenance of higher leaf water potentials during increasing drought stress.

KEYWORDS: CO₂- ENRICHMENT, ECOSYSTEMS, FIELD, GROWTH, RESPONSES

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Clinton, B.D., and J.M. Vose. 1999. Fine root respiration in mature eastern white pine (*Pinus strobus*) in situ: the importance of CO₂ in controlled environments. *Tree Physiology* 19(7):475-479.

We measured seasonal fine root respiration rate in situ while controlling

chamber temperature and [CO₂]. Atmospheric [CO₂] ([CO₂](a)) and measured soil [CO₂] ([CO₂](s)) were alternately delivered to a cuvette containing intact fine roots of eastern white pine (*Pinus strobus* L.). Respiration rates were consistently higher in [CO₂](a) than in [CO₂](s) and were almost three times higher during midsummer. Respiration rates were immediately reversed after returning to the alternate [CO₂] (i.e., [CO₂](a) --> [CO₂](s) --> [CO₂](a), and vice versa) suggesting a direct effect of elevated [CO₂] on apparent respiration. Soil-[CO₂]-based respiration rates decreased with increasing [CO₂] on a dry mass and tissue [N] basis. We conclude that estimates of soil CO₂ flux and soil carbon budgets may be improved by more completely accounting for the rhizosphere microclimate (i.e., soil temperature and [CO₂](s)) during measurement of fine root respiration.

KEYWORDS: CLIMATE, EXCHANGE, FOREST, SEEDLINGS, SOIL CARBON-DIOXIDE, TEMPERATURE, WORLD

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Colelli, G., F.G. Mitchell, and A.A. Kader. 1991. Extension of postharvest life of mission figs by CO₂-enriched atmospheres. *Hortscience* 26(9):1193-1195.

Good quality of fresh 'Mission' figs (*Ficus carica* L.) was maintained for up to 4 weeks when kept at 0, 2.2, or 5C in atmospheres enriched with 15% or 20% CO₂. The visible benefits of exposure to high CO₂ levels were reduction of decay incidence and maintenance of bright external appearance. Ethylene production was lower, and fruit softening (as measured with a deformation tester) was slower in the high-CO₂-stored figs than in those kept in air. Ethanol content of the CO₂-treated fruit increased slightly during the first 3 weeks and moderately during the 4th week, while acetaldehyde concentration increased during the first week, then decreased. The results may be applicable to the transport and storage of fresh 'Mission' figs, as high CO₂ extended their postharvest life, especially near 0C.

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Coleman, J.S., and F.A. Bazzaz. 1992. Effects of co2 and temperature on growth and resource use of cooccurring C3 and C4 annuals. *Ecology* 73(4):1244-1259.

We examined how CO₂ concentrations and temperature interacted to affect growth, resource acquisition, and resource allocation of two annual plants that were supplied with a single pulse of nutrients. Physiological and growth measurements were made on individuals of *Abutilon theophrasti* (C3) and *Amaranthus retroflexus* (C4) grown in environments with atmospheric CO₂ levels of 400 or 700- μ L/L and with light/dark temperatures of 28-degrees/22-degrees or 38-degrees/31-degrees-C. Elevated CO₂ and temperature treatments had significant independent and interactive effects on plant growth, resource allocation, and resource acquisition (i.e., photosynthesis and nitrogen uptake), and the strength and direction of these effects were often dependent on plant species. For example, final biomass of *Amaranthus* was enhanced by elevated CO₂ at 28-degrees but was depressed at 38-degrees. For *Abutilon*, elevated CO₂ increased initial plant relative growth rates at 28-degrees but not at 38-degrees, and had no significant effects on final biomass at either temperature. These results are interpreted in light of the interactive effects of CO₂ and temperature on the rates of net leaf area production and loss, and on net whole- plant nitrogen retention. At 28-degrees-C, elevated CO₂ stimulated the initial production of leaf area in both species, which led to an initial stimulation of biomass accumulation at the higher CO₂ level. However, in elevated CO₂ at 28-degrees, the rate of net leaf area loss for *Abutilon* increased while that of *Amaranthus* decreased. Furthermore, high CO₂ apparently enhanced the ability of *Amaranthus* to retain nitrogen at this temperature, which may have helped to enhance photosynthesis, whereas nitrogen retention was

unaffected in Abutilon. Thus, at 28-degrees, final biomass of Abutilon was not stimulated in a high CO₂ environment whereas the final biomass of Amaranthus was. At 38-degrees, Abutilon had slightly reduced peak leaf areas under elevated CO₂ in comparison to ambient CO₂ grown plants, but increased rates of photosynthesis per unit leaf area early in the experiment apparently compensated for reduced leaf area. For Amaranthus at 38-degrees, peak leaf area production was not affected by CO₂ treatment, but the rate of net leaf area loss hastened under elevated CO₂ conditions and was accompanied by substantial reductions of whole-plant nitrogen content and leaf photosynthesis. This may have led to the reduced biomass accumulation of high CO₂ grown plants that we observed during the last 30 d of growth. Plants of both species grown in elevated CO₂ exhibited reduced tissue-specific rates of nitrogen absorption, increased plant photosynthetic rate per unit of conductance, and increased initial allocation of biomass to roots, irrespective of temperature. Plants of both species grown under an elevated temperature regime had substantially decreased reproductive allocation, increased allocation to stem biomass, and increased plant water flux at both CO₂ treatments. The age of plants also affected our interpretations of plant responses to CO₂ and temperature treatments. For example, significant effects of CO₂ treatment on the growth of Abutilon were evident early, prior to the initiation of flowering, when nitrogen availability would have been highest and pot space would not have been limited. Nevertheless, the opposite was true for Amaranthus, in which significant effects of CO₂ treatment on plant growth were not detectable until the final 30 d of the experiment. Elevated CO₂ interacted with temperature to affect plant productivity in different ways than would have been predicted from plant responses to elevated CO₂ alone. Furthermore, a majority of the interactive effects of CO₂ concentration and temperature on plant growth could be interpreted in light of their effects on the rates of net leaf area production and loss, nitrogen retention, and, to a lesser degree, photosynthesis and resource partitioning.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO₂, C-4 PLANTS, CHENOPODIUM-ALBUM L, ELEVATED CO₂, ENRICHMENT, LEAF NITROGEN, NITROGEN-USE EFFICIENCY, OLD-FIELD ANNUALS, PHOTOSYNTHETIC RESPONSE

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Coleman, J.S., K.D.M. McConaughay, and F.A. Bazzaz. 1993. Elevated CO₂ and plant nitrogen-use - is reduced tissue nitrogen concentration size-dependent. *Oecologia* 93(2):195-200.

Plants often respond to elevated atmospheric CO₂ levels with reduced tissue nitrogen concentrations relative to ambient CO₂-grown plants when comparisons are made at a common time. Another common response to enriched CO₂ atmospheres is an acceleration in plant growth rates. Because plant nitrogen concentrations are often highest in seedlings and subsequently decrease during growth, comparisons between ambient and elevated CO₂-grown plants made at a common time may not demonstrate CO₂-induced reductions in plant nitrogen concentration per se. Rather, this comparison may be highlighting differences in nitrogen concentration between bigger, more developed plants and smaller, less developed plants. In this study, we directly examined whether elevated CO₂ environments reduce plant nitrogen concentrations independent of changes in plant growth rates. We grew two annual plant species, Abutilon theophrasti (C₃ photosynthetic pathway) and Amaranthus retroflexus (C₄, photosynthetic pathway), from seed in glass-sided growth chambers with atmospheric CO₂ levels of 350 μmol . mol⁻¹ or 700 μmol . mol⁻¹ and with high or low fertilizer applications. Individual plants were harvested every 2 days starting 3 days after germination to determine plant biomass and nitrogen concentration. We found: 1. High CO₂-grown plants had reduced nitrogen concentrations and increased biomass relative to ambient CO₂-grown plants when compared at a common time; 2. Tissue nitrogen concentrations did not vary as a function of CO₂ level when plants were

compared at a common size; and 3. The rate of biomass accumulation per rate of increase in plant nitrogen was unaffected by CO₂ availability, but was altered by nutrient availability. These results indicate that a CO₂-induced reduction in plant nitrogen concentration may not be due to physiological changes in plant nitrogen use efficiency, but is probably a size-dependent phenomenon resulting from accelerated plant growth.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ATMOSPHERES, ENRICHMENT, GROWTH, INCREASE, INSECT HERBIVORE, LEAF LITTER, NUTRITION, ROOT, SHOOT RATIO

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Coleman, J.S., L. Rochefort, F.A. Bazzaz, and F.I. Woodward. 1991. Atmospheric CO₂, plant nitrogen status and the susceptibility of plants to an acute increase in temperature. *Plant, Cell and Environment* 14(7):667-674.

Elevated levels of CO₂ in the atmosphere are expected to affect plant performance and may alter global temperature patterns. Changes in mean air temperatures that might be induced by rising levels of CO₂ and other greenhouse gases could also be accompanied by increased variability in daily temperatures such that acute increases in air temperature may be more likely than at present. Consequently, we investigated whether plants grown in a CO₂ enriched atmosphere would be differently affected by a heat shock than plants grown at ambient CO₂ levels. Plants of a C₃ annual (Abutilon theophrasti), a C₃ annual crop (Sinapis alba) and a C₄ annual (Amaranthus retroflexus) were grown from seed in growth chambers under either 400 or 700 cm³ m⁻³ CO₂, and were fertilized with either a high or low nutrient regime. Young seedlings of S. alba, as well as plants of all species in either the vegetative or reproductive phase of growth were exposed to a 4-h heat shock in which the temperature was raised an additional 14-23-degrees-C (depending on plant age). Total biomass and reproductive biomass were examined to determine the effect of CO₂, nutrient and heat shock treatments on plant performance. Heat shock, CO₂, and nutrient treatments, all had some significant effects on plant performance, but plants from both CO₂ treatments responded similarly to heat shocks. We also found, as expected, that plants grown under high CO₂ had dramatically decreased tissue N concentrations relative to plants grown under ambient conditions. We predicted that high- CO₂-grown plants would be more susceptible to a heat shock than ambient-CO₂-grown plants, because the reduced N concentrations of high-CO₂ grown plants could result in the reduced synthesis of heat shock proteins and reduced thermotolerance. Although we did not examine heat shock proteins, our results showed little relationship between plant nitrogen status and the ability of a plant to tolerate an acute increase in temperature.

KEYWORDS: C-3, ELEVATED CO₂, ENRICHMENT, GROWTH, HEAT-SHOCK PROTEINS, INSECT HERBIVORE, RESPONSES, THERMOTOLERANCE

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Coleman, W.K., and J. McInerney. 1997. Enhanced dormancy release and emergence from potato tubers after exposure to a controlled atmosphere. *American Potato Journal* 74(3):173-182.

The North American potato industry requires an effective and environmentally-appropriate, dormancy-release methodology. The present study examined dormancy release and subsequent sprout emergence based on a modified, controlled-atmosphere (CA) approach using such environmentally-compatible gases as nitrogen, carbon dioxide and oxygen with or without trace amounts of ethylene (50 ppm). This paper is the first published report of a semi-automated, controlled-atmosphere system for dormancy release of potato tubers. The system allows computer- controlled gas application and analysis for up to four gas mixtures simultaneously. Low oxygen concentrations (<10%) for 10

days in the presence of 10 to 60% carbon dioxide or a high carbon dioxide (60%)/oxygen (40%) treatment caused tuber break-down regardless of cultivar. The most effective mixtures for enhanced dormancy release and sprout emergence were 20% CO₂/40% O₂ or 60% CO₂/18-20% O₂ and their effects were further enhanced by 50 ppm C₂H₄ (ethylene). In the presence of 50 ppm C₂H₄, the 20% CO₂/40% O₂ mixture was comparable to bromoethane in effectiveness. Temperature and light exposure affected subsequent Russet Burbank tuber responses to CO₂/O₂/C₂H₄ gas mixtures.

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Coley, P.D. 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climatic Change* 39(2-3):455-472.

The interactions between plants and herbivores are key determinants of community structure world wide. Their role is particularly important in lowland tropical rain forests where rates of herbivory are higher, plants are better defended chemically and physically, and herbivores have specialized diets. In contrast to the temperate zone, most of the herbivory in the tropics occurs on ephemeral young leaves (>70%), which requires herbivores to have finely tuned host-finding abilities. As a consequence of these tight ecological and evolutionary linkages, the interplay between plants and herbivores in the tropics may be more susceptible to perturbations of climate change. Increases in global temperature, atmospheric CO₂, and the length of the dry season are all likely to have ramifications for plant/herbivore interactions in the tropics. Here I extrapolate from our current and incomplete understanding of the mechanisms regulating plant/herbivore interactions and present a scenario for possible trends under a changing climate. Although elevated CO₂ tends to enhance plant growth rates, the larger effects of increased drought stress will probably result in lower growth. In atmospheres experimentally enriched in CO₂, the nutritional quality of leaves declines substantially due to a dilution of nitrogen by 10-30%. This response is buffered in plant species associated with nitrogen fixers. Elevated CO₂ should also cause a slight decrease in nitrogen-based defenses (e.g., alkaloids) and a slight increase in carbon-based defenses (e.g., tannins). The most dramatic and robust predicted effect of climate change is on rates of herbivory. Lower foliar nitrogen due to CO₂ fertilization of plants causes an increase in consumption per herbivore by as much as 40% and unusually severe drought appears to cause herbivore populations to explode. In areas where elevated CO₂ is combined with drying, rates of herbivory may rise 2-4 fold. The frequency of insect outbreaks is also expected to increase. Higher herbivory should further reduce plant growth rates, perhaps favoring plant species that are well-defended or fix nitrogen. The predicted increase in the number of herbivores is primarily due to relaxed pressure from predators and parasitoids. Elevated temperatures may increase herbivore developmental times, affording them partial escape from discovery by natural enemies, and drought appears to decimate parasitoid populations. The expected decline in parasitoid numbers may be due to direct effects of dry season drought or to the relative scarcity of herbivores during that period. As a consequence, the relative abundance of species will change, and overall biodiversity should decline.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ELEVATED ATMOSPHERIC CO₂, INSECT HERBIVORE INTERACTIONS, LEAF PRODUCTION, LONG-TERM EXPOSURE, MULTIPLE ALLELOCHEMICALS, PAPER BIRCH, PERFORMANCE, PLANT, UNDERSTORY COMMUNITY

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Colinvaux, P.A. 1998. A new vicariance model for Amazonian endemics. *Global Ecology and Biogeography Letters* 7(2):95-96.

It is unlikely that ice age climates of the Amazon were sufficiently arid to fragment the forest as required by the Haffer refugial hypothesis. However, glacial Amazon climates were colder and had reduced CO₂ concentrations that would have had their strongest effects on the biota in the elevated areas stipulated to have been refugia. If local endemism of butterflies or birds records Pleistocene speciation, this is because glacial climates provided cool, CO₂ starved islands in a sea of continuous forest.

KEYWORDS: TEMPERATURE DEPRESSION

415

Combe, L., J.M. Bertolini, and P. Quetin. 1993. Effects of carbon-dioxide and light on photosynthesis of primrose (*primula-obconica* hance). *Canadian Journal of Plant Science* 73(4):1149-1161.

Net CO₂ exchange rates were measured on a 1 m² crop of *Primula obconica* placed in a closed loop growing chamber as a function of irradiation and CO₂ concentration. Greenhouse cultivation with CO₂ enrichment (700 ppm) or without (350 ppm) had only very little effect on dry weight or on flowering rate and did not modify photosynthetic capacity of primrose. Productivity differences between horticultural techniques, such as supplemental lighting and/or CO₂ enrichment, can be partly explained by study of photosynthesis curves: light increase is more efficient than carbon dioxide increase, the latter giving the best results with young primroses under strong irradiation.

KEYWORDS: ACCLIMATION, CARBOXYLASE, ELEVATED CO₂, ENRICHMENT, ENVIRONMENTS, GAS-EXCHANGE, GROWTH, HIGH ATMOSPHERIC CO₂, TEMPERATURE, YIELD

416

Comins, H.N. 1994. Equilibrium-analysis of integrated plant-soil models for prediction of the nutrient limited growth-response to CO₂ enrichment. *Journal of Theoretical Biology* 171(4):369-385.

Although higher ambient CO₂ concentration is known to promote increased plant productivity under optimal growing conditions, it is not obvious if there will be a sustained growth response in natural and plantation ecosystems, where other resources, such as nutrients, may become limiting. Comins and McMurtrie (1993, *Ecol. Applic.* 3, 666-681) have constructed the G'DAY (Generic Decomposition A nd Field) integrated plant-soil model to investigate this CO₂-nutrient interaction, and have described an analytic method for predicting the long-term response of their model to a step change in CO₂ concentration, using the analytic "two timing" approximation. This analysis gives insights into the interactions of the numerous parameters in a comprehensive plant-soil model, and may be generalizable to other such models. The current paper explores the accuracy of the approximation, and discusses various generalizations of the basic model to which the analytic model can still be applied. The very long-term CO₂ response of G'DAY was predicted by considering the dynamics of the passive soil organic matter pool in the "two timing" approximation. It was found that the two-timing approximation underestimates the 50-100 year CO₂ response in systems that lose a very small proportion of nitrogen per recycling cycle. The other areas considered here are as follows. (i) More complex relationships between N:C ratios and carbon allocation fractions for plant organs, including variable heartwood N:C ratio (which has been identified as an important determinant of long-term CO₂ response). Typical results are presented for a range of sensitivities of heartwood N:C ratio to changes in foliar N:C ratio. (ii) Variants of the CENTURY soil model were examined, having variable N:C ratios in the soil organic matter pools and/or carbon flux partition fractions influenced by N:C ratios. (iii) Results are presented for a preliminary analysis of variable nitrogen fixation.

KEYWORDS: CLIMATE, DECOMPOSITION, ECOSYSTEMS, FORESTS, GRASSLANDS

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Comins, H.N., and R.E. McMurtrie. 1993. Long-term response of nutrient-limited forests to CO₂ enrichment - equilibrium behavior of plant-soil models. *Ecological Applications* 3(4):666-681.

Established process-based models of forest biomass production in relation to atmospheric CO₂ concentration (McMurtrie 1991) and soil carbon/nutrient dynamics (Parton et al. 1987) are integrated to derive the "Generic Decomposition and Yield" model (G'DAY). The model is used to describe how photosynthesis and nutritional factors interact to determine the productivity of forests growing under nitrogen-limited conditions. A simulated instantaneous doubling of atmospheric CO₂ concentration leads to a growth response that is initially large (27% above productivity at current CO₂) but declines to <10% elevation within 5 yr. The decline occurs because increases in photosynthetic carbon gain at elevated CO₂ are not matched by increases in nutrient supply. Lower foliar N concentrations at elevated CO₂ have two countervailing effects on forest production: decreased rates of N cycling between vegetation and soils (with negative consequences for productivity), and reduced rates of N loss through gaseous emission, fire, and leaching. Theoretical analysis reveals that there is an enduring response to CO₂ enrichment, but that the magnitude of the long-term equilibrium response is extremely sensitive to the assumed rate of gaseous emission resulting from mineralization of nitrogen. Theory developed to analyze G'DAY is applicable to other published production-decomposition models describing the partitioning of soil carbon among compartments with widely differing decay-time constants.

KEYWORDS: CLIMATE, COMMUNITIES, DYNAMICS, ELEVATED ATMOSPHERIC CO₂, ESTUARINE MARSH, GRASSLANDS, GROWTH, PRODUCTIVITY, TEMPERATURE, TERRESTRIAL ECOSYSTEMS

418

Conroy, J.P. 1992. Influence of elevated atmospheric CO₂ concentrations on plant nutrition. *Australian Journal of Botany* 40(4-5):445-456.

The rising levels of atmospheric CO₂ are likely to increase biomass production of C3 species in both natural and managed ecosystems because photosynthetic rates will be higher. The greatest absolute increase in productivity will occur when nitrogen and phosphorus availability in the soil is high. Low nitrogen does not preclude a growth response to high CO₂, whereas some C3 species fail to respond to high CO₂ when phosphorus is low, possibly because insufficient phosphorus is available to maintain maximum photosynthetic activity at high CO₂. C3 plants respond to high CO₂ because the flux of carbon through the photo-reductive cycle is increased and photorespiration is suppressed. This change in metabolism appears to alter the foliar nutrient concentration required to promote maximum productivity (critical concentration). Higher phosphorus concentrations are needed at elevated CO₂, whereas the nitrogen requirement is reduced by CO₂ enrichment. Since critical concentrations are used to evaluate nutrient status of crop and forest species and to manage fertiliser programs, they will need reassessing as the atmospheric CO₂ concentration rises. Another consequence of the altered nutrient requirement at high CO₂ is that the nitrogen concentrations of foliage, roots and grain are consistently lower in plants grown at elevated CO₂, irrespective of availability of nitrogen in the soil. In natural ecosystems, the lower nitrogen to carbon ratio of the litter may alter rates of nutrient cycling. For farmers, the rising CO₂ concentrations could cause reductions in grain nitrogen, and therefore protein content. This could have important implications for baking quality of hard wheats as well as affecting the nutrient value of grain

such as rice.

KEYWORDS: C-3, CARBON DIOXIDE, ENRICHMENT, GROWTH, NITROGEN CONCENTRATIONS, PHOTOSYNTHESIS, RADIATA DON, STRESS, WATER-USE, WHEAT

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Conroy, J.P. 1993. Influence of elevated atmospheric CO₂ concentrations on plant nutrition (vol 40, pg 445, 1992). *Australian Journal of Botany* 41(1):143.

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Conroy, J., and P. Hocking. 1993. Nitrogen nutrition of C-3 plants at elevated atmospheric CO₂ concentrations. *Physiologia Plantarum* 89(3):570-576.

The atmospheric CO₂ concentration has risen from the preindustrial level of approximately 290 $\mu\text{mol mol}^{-1}$ to more than 350 $\mu\text{mol mol}^{-1}$ in 1993. The current rate of rise is such that concentrations of 420 $\mu\text{mol mol}^{-1}$ are expected in the next 20 years. For C-3 plants, higher CO₂ levels favour the photosynthetic carbon reduction cycle over the photorespiratory cycle, resulting in higher rates of carbohydrate production and plant productivity. The change in balance between the two photosynthetic cycles appears to alter nitrogen and carbon metabolism in the leaf, possibly causing decreases in nitrogen concentrations in the leaf. This may result from increases in the concentration of storage carbohydrates of high molecular weight (soluble or insoluble) and/or changes in distribution of protein or other nitrogen containing compounds. Uptake of nitrogen may also be reduced at high CO₂ due to lower transpiration rates. Decreases in foliar nitrogen levels have important implications for production of crops such as wheat, because fertilizer management is often based on leaf chemical analysis, using standards estimated when the CO₂ levels were considerably lower. These standards will need to be re-evaluated as the CO₂ concentration continues to rise. Lower levels of leaf nitrogen will also have implications for the quality of wheat grain produced, because it is likely that less nitrogen would be retranslocated during grain filling.

KEYWORDS: ACCLIMATION, CARBOHYDRATE, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, MINERAL NUTRITION, NITRATE, PHOTOSYNTHESIS, WHEAT

421

Conroy, J.P., P.J. Milham, and E.W.R. Barlow. 1992. Effect of nitrogen and phosphorus availability on the growth- response of eucalyptus-grandis to high CO₂. *Plant, Cell and Environment* 15(7):843-847.

The response of Eucalyptus grandis seedlings to elevated atmospheric CO₂ concentrations was examined by growing seedlings at either 340 or 660- $\mu\text{mol CO}_2 \text{ mol}^{-1}$ for 6 weeks. Graded increments of phosphorus and nitrogen fertilizers were added to a soil deficient in these nutrients to establish if the growth response to increasing nutrient availability was affected by CO₂ concentration. At 660- $\mu\text{mol CO}_2 \text{ mol}^{-1}$, seedling dry weight was up to five times greater than at 340- $\mu\text{mol CO}_2 \text{ mol}^{-1}$. The absolute response was largest when both nitrogen and phosphorus availability was high but the relative increase in dry weight was greatest at low phosphorus availability. At 340- $\mu\text{mol CO}_2 \text{ mol}^{-1}$ and high nitrogen availability, growth was stimulated by addition of phosphorus up to 76 mg kg⁻¹ soil. Further additions of phosphorus had little effect. However, at 660- $\mu\text{mol CO}_2 \text{ mol}^{-1}$, growth only began to plateau at a phosphorus addition rate of 920 mg kg⁻¹ soil. At 340- $\mu\text{mol CO}_2 \text{ mol}^{-1}$ and high phosphorus availability, increasing nitrogen from 40 to 160 mg kg⁻¹ soil had little effect on plant growth. At high CO₂, growth

reached a maximum at between 80 and 160 mg nitrogen kg⁻¹ soil. Total uptake of phosphorus was greater at high CO₂ concentration at all fertilizer addition rates, but nitrogen uptake was either lower or unchanged at high CO₂ concentration except at the highest nitrogen fertilizer rate. The shoot to root ratio was increased by CO₂ enrichment, primarily because the specific leaf weight was greater. The nitrogen and phosphorus concentration in the foliage was lower at elevated CO₂ concentration partly because of the higher specific leaf weight. These results indicate that critical foliar concentrations currently used to define nutritional status and fertilizer management may need to be reassessed as the atmospheric CO₂ concentration rises.

KEYWORDS: CARBON DIOXIDE, DEFICIENCY, ENRICHMENT, METABOLISM, PLANTS, RADIATA D-DON, SEEDLINGS, STRESS, WHEAT

422

Conroy, J.P., P.J. Milham, D.I. Bevege, and E.W.R. Barlow. 1990. Influence of phosphorus deficiency on the growth-response of 4 families of *Pinus radiata* seedlings to CO₂-enriched atmospheres. *Forest Ecology and Management* 30(1-4):175-188.

423

Conroy, J.P., P.J. Milham, M. Mazur, and E.W.R. Barlow. 1990. Growth, dry-weight partitioning and wood properties of *Pinus radiata* d don after 2 years of CO₂ enrichment. *Plant, Cell and Environment* 13(4):329-337.

424

Conroy, J.P., P.J. Milham, M.L. Reed, and E.W. Barlow. 1990. Increases in phosphorus requirements for CO₂-enriched pine species. *Plant Physiology* 92(4):977-982.

425

Conroy, J.P., S. Seneweera, A.S. Basra, G. Rogers, and B. Nissenwooller. 1994. Influence of rising atmospheric CO₂ concentrations and temperature on growth, yield and grain quality of cereal crops. *Australian Journal of Plant Physiology* 21(6):741-758.

A possible scenario for the end of the 21st century is that the atmospheric CO₂ concentration will be in the range of 510-760 μL L⁻¹ and that the mean global temperature will be 1.5-4.5 degrees C higher. Further, there may be greater incidences of extreme climatic events, which together with the CO₂ and temperature changes will influence development, growth and grain yield of cereals such as rice and wheat. For these C-3, plants, the driving force for the growth response to elevated CO₂ is higher leaf CO₂ assimilation rates (4). However, the response of A to CO₂ depends on temperature with maximum absolute increases occurring at temperatures which do not cause flower abortion, while negligible increases are observed at low temperatures. At high temperatures, where A is reduced because of partial inactivation of photosynthetic enzymes, the increase in A due to CO₂ enrichment is still observed. Other factors, such as changes in shoot water relations or hormone concentrations, may influence growth at elevated CO₂ concentrations. Wheat and rice development is accelerated by high temperature and consequently grain yield is reduced because there is less time for radiation to be intercepted during the vegetative phase. Although high CO₂ also accelerates development in rice and, to a lesser extent in wheat, the extra carbohydrate produced by increases in A results in at least a 40% increase in grain yield at temperatures which do not cause flower abortion. This is due mainly to increased tiller

numbers rather than increases in the number or weight of individual grains. However, the yield enhancement due to high CO₂ will not necessarily compensate for decreases in yield caused by accelerated development at high temperatures. As predicted by the response of A to high CO₂, the relative increase in yield, due to rising CO₂ concentrations, is smaller at lower temperatures. Elevated atmospheric CO₂ may improve the tolerance of plants to heat-induced drought stress by facilitating the maintenance of cell volume and photosynthetic function in the leaves. Increased carbohydrate storage in the stems may also be an advantage during grain filling if the flag leaves senesce prematurely. However, it is unlikely that the effect of very high temperatures on newer abortion will be ameliorated by high CO₂. For bread making, the quality of flour produced from grain developed at high temperatures is poorer. High CO₂ may also have an effect through a reduction in the protein content of wheat grain. For rice, the amylose content of the grain, a major determinant of cooking quality is increased under elevated CO₂.

KEYWORDS: C-3 PLANTS, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO₂, NITROGEN, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANT GROWTH, RICE, WATER RELATIONS, WHEAT PLANTS

426

Constable, J.V.H., A.B. Guenther, D.S. Schimel, and R.K. Monson. 1999. Modelling changes in VOC emission in response to climate change in the continental United States. *Global Change Biology* 5(7):791-806.

The alteration of climate is driven not only by anthropogenic activities, but also by biosphere processes that change in conjunction with climate. Emission of volatile organic compounds (VOCs) from vegetation may be particularly sensitive to changes in climate and may play an important role in climate forcing through their influence on the atmospheric oxidative balance, greenhouse gas concentration, and the formation of aerosols. Using the VEMAP vegetation database and associated vegetation responses to climate change, this study examined the independent and combined effects of simulated changes in temperature, CO₂ concentration, and vegetation distribution on annual emissions of isoprene, monoterpenes, and other reactive VOCs (ORVOCs) from potential vegetation of the continental United States. Temperature effects were modelled according to the direct influence of temperature on enzymatic isoprene production and the vapour pressure of monoterpenes and ORVOCs. The effect of elevated CO₂ concentration was modelled according to increases in foliar biomass per unit of emitting surface area. The effects of vegetation distribution reflects simulated changes in species spatial distribution and areal coverage by 21 different vegetation classes. Simulated climate warming associated with a doubled atmospheric CO₂ concentration enhanced total modelled VOC emission by 81.8% (isoprene + 82.1%, monoterpenes + 81.6%, ORVOC + 81.1%), whereas a simulated doubled CO₂ alone enhanced total modelled VOC emission by only + 11.8% (isoprene + 13.7%, monoterpenes + 4.1%, ORVOC + 11.7%). A simulated redistribution of vegetation in response to altered temperatures and precipitation patterns caused total modelled VOC emission to decline by 10.4% (isoprene - 11.7%, monoterpenes -18.6%, ORVOC 0.0%) driven by a decline in area covered by vegetation classes emitting VOCs at high rates. Thus, the positive effect of leaf-level adjustments to elevated CO₂ (i.e. increases in foliar biomass) is balanced by the negative effect of ecosystem-level adjustments to climate (i.e. decreases in areal coverage of species emitting VOC at high rates).

KEYWORDS: AEROSOL FORMATION, ALPHA- PINENE, BETA- PINENE, BIOGENIC EMISSIONS, CARBON DIOXIDE, ELEVATED CO₂, FOREST, GROWTH, ISOPRENE, ORGANIC-COMPOUND EMISSIONS

427

Constable, J.V.H., M.E. Litvak, J.P. Greenberg, and R.K. Monson. 1999. Monoterpene emission from coniferous trees in response to elevated CO₂ concentration and climate warming. *Global Change Biology* 5(3):255-267.

It was hypothesized that high CO₂ availability would increase monoterpene emission to the atmosphere. This hypothesis was based on resource allocation theory which predicts increased production of plant secondary compounds when carbon is in excess of that required for growth. Monoterpene emission rates were measured from needles of (a) Ponderosa pine grown at different CO₂ concentrations and soil nitrogen levels, and (b) Douglas fir grown at different CO₂ concentrations. Ponderosa pine grown at 700 $\mu\text{mol mol}^{-1}$ CO₂ exhibited increased photosynthetic rates and needle starch to nitrogen (N) ratios when compared to trees grown at 350 $\mu\text{mol mol}^{-1}$ CO₂. Nitrogen availability had no consistent effect on photosynthesis. Douglas fir grown at 550 $\mu\text{mol mol}^{-1}$ CO₂ exhibited increased photosynthetic rates as compared to growth at 350 $\mu\text{mol mol}^{-1}$ CO₂ in old, but not young needles, and there was no influence on the starch/N ratio. In neither species was there a significant effect of elevated growth CO₂ on needle monoterpene concentration or emission rate. The influence of climate warming and leaf area index LAI on monoterpene emission were also investigated. Douglas fir grown at elevated CO₂ plus a 4 degrees C increase in growth temperature exhibited no change in needle monoterpene concentration, despite a predicted 50% increase in emission rate. At elevated CO₂ concentration the LAI increased in Ponderosa pine, but not Douglas fir. The combination of increased LAI and climate warming are predicted to cause an 80% increase in monoterpene emissions from Ponderosa pine forests and a 50% increase in emissions from Douglas fir forests. This study demonstrates that although growth at elevated CO₂ may not affect the rate of monoterpene emission per unit biomass, the effect of elevated CO₂ on LAI, and the effect of climate warming on monoterpene biosynthesis and volatilization, could increase canopy monoterpene emission rate.

KEYWORDS: ATMOSPHERIC CHEMISTRY, CARBON, GROWTH, ISOPRENE, NITROGEN, PONDEROSA PINE, RATE VARIABILITY, SEEDLINGS

428

Constable, J.V.H., G.E. Taylor, J.A. Laurence, and J.A. Weber. 1996. Climatic change effects on the physiology and growth of *Pinus ponderosa*: Expectations from simulation modeling. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 26(8):1315-1325.

The TREGRO model was used to simulate the growth response of mature *Pinus ponderosa* Dougl. ex Laws. to the interacting effects of changes in CO₂ (+200 $\mu\text{mol L}^{-1}$), temperature (+4 degrees C), and O₃ (0.5x, 1x, and 2x ambient). Relative to simulated growth under the base-line climate in Corvallis, Oregon, elevated CO₂ and temperature individually increased total-tree biomass gain by 29% and 13%, respectively, but when combined increased biomass gain by 49%. Ozone at all exposures reduced total-tree biomass gain by 1%, 19%, and 39%, respectively, as compared with simulated base-line conditions. Elevated CO₂ increased photosynthesis and reduced stomatal conductance and partially offset growth reductions due to 2x O₃. Elevated temperature, however, increased both photosynthesis and stomatal conductance and was less effective at mitigating growth reductions due to 2x O₃. Growth at 2x O₃ in elevated CO₂ and temperature conditions had little effect on total-tree growth, but decreased fine-root growth by 61%. The simulated changes in stomatal conductance and fine-root biomass are expected to interact with the availability of soil resources to affect tree growth and possibly alter the distribution of *Pinus ponderosa*.

KEYWORDS: COMPENSATORY RESPONSES, DROUGHT,

ELEVATED CO₂, GAS-EXCHANGE, NET PHOTOSYNTHESIS, OZONE EXPOSURE, PHOTOSYNTHETIC CAPACITY, STOMATAL CONDUCTANCE, STRESSES, USE EFFICIENCY

429

Conway, T.J., L.P. Steele, and P.C. Novelli. 1993. Correlations among atmospheric CO₂, CH₄ and CO in the arctic, march 1989. *Atmospheric Environment Part A-General Topics* 27(17-18):2881-2894.

During six aircraft flights conducted as part of the third Arctic Gas and Aerosol Sampling Program (AGASP III, March 1989), 189 air samples were collected throughout the Arctic troposphere and lower stratosphere for analysis of CO₂, CH₄ and CO. The mixing ratios of the three gases varied significantly both horizontally and vertically. Elevated concentrations were found in layers with high anthropogenic aerosol concentrations (Arctic Haze). The mixing ratios of CO₂, CH₄ and CO were highly correlated on all flights. A linear regression of CH₄ vs CO₂ for pooled data from all flights yielded a correlation coefficient ($r(2)$) of 0.88 and a slope of 13.5 ppb CH₄/ppm CO₂ ($n = 186$). For CO vs CO₂ a pooled linear regression gave $r(2) = 0.91$ and a slope of 15.8 ppb CO/ppm CO₂ ($n = 182$). Carbon dioxide, CH₄ and CO also exhibited mean vertical gradients with slopes of 0.37, -4.4 and -4.2 ppb km⁻¹, respectively. Since the carbon dioxide variations observed in the Arctic atmosphere during winter are due primarily to variations in the emissions and transport of anthropogenic CO₂ from Europe and Asia, the strong correlations that we have found suggest that a similar interpretation applies to CH₄ and CO. Using reliable estimates of CO₂ emissions for the source regions and the measured CH₄/CO₂ and CO/CO₂ ratios, we estimate a regional European CH₄ source of 47+/-6 Tg CH₄ yr⁻¹ that may be associated with fossil fuel combustion. A similar calculation for CO results in an estimated regional CO source of 82+/- 2Tg CO yr⁻¹.

KEYWORDS: AEROSOL, AGASP, AIR-POLLUTION, ALASKA, APRIL, ARCTIC HAZE, BARROW, CARBON DIOXIDE, METHANE, VARIABILITY

430

Cook, A.C., D.T. Tissue, S.W. Roberts, and W.C. Oechel. 1998. Effects of long-term elevated [CO₂] from natural CO₂ springs on *Nardus stricta*: Photosynthesis, biochemistry, growth and phenology. *Plant, Cell and Environment* 21(4):417-425.

Plants of *Nardus stricta* growing near a cold, naturally emitting CO₂ spring in Iceland were used to investigate the long-term (> 100 years) effects of elevated [CO₂] on photosynthesis, biochemistry, growth and phenology in a northern grassland ecosystem. Comparisons were made between plants growing in an atmosphere naturally enriched with CO₂ (approximate to 790 $\mu\text{mol mol}^{-1}$) near the CO₂ spring and plants of the same species growing in adjacent areas exposed to ambient CO₂ concentrations (approximate to 360 $\mu\text{mol mol}^{-1}$). *Nardus stricta* growing near the spring exhibited earlier senescence and reductions in photosynthetic capacity (approximate to 25%), Rubisco content (approximate to 26%), Rubisco activity (approximate to 40%), Rubisco activation state (approximate to 23%), chlorophyll content (approximate to 33%) and leaf area index (approximate to 22%) compared with plants growing away from the spring. The potential positive effects of elevated [CO₂] on grassland ecosystems in Iceland are likely to be reduced by strong down-regulation in the photosynthetic apparatus of the abundant *N. stricta* species.

KEYWORDS: ACCLIMATION, ALASKAN TUSsock TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, CARBOXYLASE ACTIVITY, ENRICHMENT, ERIOPHORUM VAGINATUM, PLANTS, RESPONSES, RUBISCO, SEEDLINGS

431

Corey, K.A., M.E. Bates, and S.L. Adams. UNKNOWN YEAR. Carbon-dioxide exchange of lettuce plants under hypobaric conditions. *Physical, Chemical, Biochemical and Biological Techniques and Processes* :301-308.

Growth of plants in a Controlled Ecological Life Support System (CELSS) may involve the use of hypobaric pressures enabling lower mass requirements for atmospheres and possible enhancement of crop productivity. A controlled environment plant growth chamber with hypobaric capability designed and built at Ames Research Center was used to determine if reduced pressures influence the rates of photosynthesis (Ps) and dark respiration (DR) of hydroponically grown lettuce plants. The chamber, referred to as a plant volatiles chamber (PVC), has a growing area of about 0.2 m², a total gas volume of about 0.7 m³, and a leak rate at 50 kPa of < 0.1%/day. When the pressure in the chamber was reduced from ambient to 51 kPa, the rate of net Ps increased by 25% and the rate of DR decreased by 40%. The rate of Ps increased linearly with decreasing pressure. There was a greater effect of reduced pressure at 41 Pa CO₂ than at 81 Pa CO₂. This is consistent with reports showing greater inhibition of photorespiration (Pr) in reduced O₂ at low CO₂ concentrations. When the partial pressure of O₂ was held constant but the total pressure was varied between 51 and 101 kPa, the rate of CO₂ uptake was nearly constant, suggesting that low pressure enhancement of Ps may be mainly attributable to lowered partial pressure of O₂ and the accompanying reduction in Pr. The effects of lowered partial pressure of O₂ on Ps and DR could result in substantial increases in the rates of biomass production, enabling rapid throughput of crops or allowing flexibility in the use of mass and energy resources for a CELSS.

KEYWORDS: INCOMPLETE, ENVIRONMENTS, PRODUCTIVITY, WHEAT

432

Corlett, R.T., and J.V. LaFrankie. 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic Change* 39(2-3):439-453.

Changes in plant phenology will be one of the earliest responses to rapid global climate change and could potentially have serious consequences both for plants and for animals that depend on periodically available plant resources. Phenological patterns are most diverse and least understood in the tropics. In those parts of tropical Asia where low temperature or drought impose a seasonal rest period, regular annual cycles of growth and reproduction predominate at the individual, population, and community level. In aseasonal areas, individuals and populations show a range of sub- to supra-annual periodicities, with an overall supra-annual reproductive periodicity at the community level. There is no evidence for photoperiod control of phenology in the Asian tropics, and seasonal changes in temperature are a likely factor only near the northern margins. An opportunistic response to water availability is the simplest explanation for most observed patterns where water is seasonally limiting, while the great diversity of phenological patterns in the aseasonal tropics suggests an equal diversity of controls. The robustness of current phenological patterns to high interannual and spatial variability suggests that most plant species will not be seriously affected by the phenological consequences alone of climate change. However, some individual plant species may suffer, and the consequences of changes in plant phenology for flower- and fruit-dependent animals in fragmented forests could be serious.

KEYWORDS: ASEASONAL TROPICS, CONSEQUENCES, COSTA-RICA, DRY FOREST, ELEVATED CO₂, MOIST FOREST, PATTERNS, RAIN-FOREST, REPRODUCTIVE PHENOLOGY, TREES

433

Cornelissen, J.H.C., A.L. Carnelli, and T.V. Callaghan. 1999. Generalities in the growth, allocation and leaf quality responses to elevated CO₂ in eight woody species. *New Phytologist* 141(3):401-409.

This paper reports general patterns of relative growth rate and related traits in response to elevated atmospheric CO₂ in eight woody species ranging widely in life form, leaf habit, taxonomy and ecology. Young plants of these species, all of comparable ontogenetic phases, were grown simultaneously in large containers with favourable nutrient and water availability in transparent outdoor chambers at 350 and 700 μ mol l⁻¹ CO₂ for one growing season. We found the following consistent responses. (1) All species grew faster at elevated CO₂, whereas the following leaf and allocation traits were consistently lower in CO₂-enriched environments: specific leaf area (quotient of leaf area and leaf weight), leaf area ratio (quotient of total leaf area and plant weight), weight-based foliar N concentration and, to a smaller extent, leaf weight fraction (quotient of leaf weight and plant weight). (2) There was important interspecific variation in the magnitude of the response of relative growth rate to CO₂. Specific leaf area at ambient CO₂ explained 88% of the variation in relative growth rate response to CO₂ among the eight species. At ambient CO₂, relative growth rate itself, was significantly correlated with the relative growth rate response to CO₂ only if the leafless species *Ulex gallii* was excluded from analysis. (3) The four deciduous species had a significantly stronger relative growth rate response to CO₂ than the four evergreens. This corresponded with their generally higher specific leaf area. (4) Specific leaf area and leaf habit might be useful for scaling up exercises, as easy-to-measure substitutes for growth responses of (woody) vegetation to elevated CO₂. However, the usefulness of such traits in this context needs to be tested in realistic, longer-term manipulative experiments in real ecosystems.

KEYWORDS: ATMOSPHERIC CO₂, CARBONDIOXIDE, CHEMICAL-COMPOSITION, ECOSYSTEMS, MODEL, NITROGEN, PLANT-RESPONSES, SEEDLINGS, TREE, WIDE-RANGE

434

Corrigan, V.K., and A. Carpenter. 1993. Effects of treatment with elevated carbon-dioxide levels on the sensory quality of asparagus. *New Zealand Journal of Crop and Horticultural Science* 21(4):349-357.

Asparagus spears (*Asparagus officinalis* L. cv. Limbras 10) were stored for 3-5 days in atmospheres containing between 40 and 90% carbon dioxide (CO₂) to evaluate the effect of insecticidal CO₂ atmospheres on sensory quality based on sensory panel ratings of characteristic asparagus flavour, off-flavours, flavour acceptability, and overall acceptability. Sensory quality of spears after 4 days storage in 60% CO₂ was similar to air-stored spears but 5 days storage caused deterioration in the CO₂-stored spears relative to the air-stored spears. Using higher CO₂ levels than this for shorter storage times resulted in spears with CO₂ injury and poor sensory quality. Spear quality deteriorated with shelf period but previous CO₂ treatment did not affect the rate of deterioration. Storing spears at 5-degrees-C in 60% CO₂ or 0-degrees-C in air gave consistently higher (lower for off-flavours) sensory quality ratings for all characteristics assessed than vice versa. Thick spears had more flavour and were more acceptable than thin spears. Thick spears had more flavour than thin spears when stored in CO₂, but thin spears had more flavour when stored in air than in CO₂. In 60% CO₂, spears stored dry had a more acceptable flavour and were more acceptable overall (where panellists considered aspects such as flavour, texture, and off-flavours in the overall rating) than those stored with their butts in water. Spears stored in air with their butts in water had a more acceptable flavour and were more acceptable overall, spears stored with their butts in water had less characteristic asparagus flavour than those stored dry. High levels of CO₂ could be used as a disinfection treatment of fresh asparagus spears without significant effect on spear quality (compared to spears stored in air under similar conditions).

providing levels >60% CO₂ are not used, and storage time in the atmosphere is kept to 4 days or less.

KEYWORDS: CONTROLLED-ATMOSPHERE STORAGE, HARVEST, SPEARS

435

Cotrufo, M.E., and P. Ineson. 1995. Effects of enhanced atmospheric CO₂ and nutrient supply on the quality and subsequent decomposition of fine roots of betula- pendula roth and picea-sitchensis (bong) carr. *Plant and Soil* 170(2):267-277.

Fine root litter derived from birch (*Betula pendula* Roth.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plants grown under two CO₂ atmospheric concentrations (350 ppm and 600 ppm) and two nutrient regimes was used for decomposition studies in laboratory microcosms. Although there were interactions between litter type, CO₂/fertiliser treatments and decomposition rates, in general, an increase in the C/N ratio of the root tissue was observed for roots of both species grown under elevated CO₂ in unfertilized soil. Both weight loss and respiration of decomposing birch roots were significantly reduced in materials derived from enriched CO₂, whilst the decomposition of spruce roots showed no such effect. A parallel experiment was performed using *Betula pendula* root litter grown under different N regimes, in order to test the relationship between C/N ratio of litter and root decomposition rate. A highly significant ($p < 0.001$) negative correlation between C/N ratio and root litter respiration was found, with an $r(2) = 0.97$. The results suggest that the increased C/N ratio of plant tissues induced by elevated CO₂ can result in a reduction of decomposition rate, with a resulting increase in forest soil C stores.

KEYWORDS: ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, ENRICHMENT, FERTILIZATION, FOREST, GROWTH, NITROGEN, ORGANIC-MATTER, PINE, RESPONSES

436

Cotrufo, M.F., M.J.I. Briones, and P. Ineson. 1998. Elevated CO₂ affects field decomposition rate and palatability of tree leaf litter: Importance of changes in substrate quality. *Soil Biology and Biochemistry* 30(12):1565-1571.

Field decomposition rates of ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.) leaf litters were measured for litters grown at ambient and elevated concentration of atmospheric CO₂ inside solar domes. Litter raised at 600 $\mu\text{l l}^{-1}$ CO₂ retained significantly more mass at the end of the first year of field decomposition than material raised at 350 $\mu\text{l l}^{-1}$. This reduction in decomposition could be related to changes in tissue quality resulting from growing the plants at higher CO₂ concentrations, with C-to-N ratios and lignin contents being significantly increased. The elevated CO₂ treatment also affected the rate of consumption of ash leaf litter by *Oniscus asellus* L. (Isopoda: Oniscoidea), with significantly less (-16%) material being consumed for litter derived from the high CO₂ regime. Our results indicate that changes in litter quality, which we may expect under elevated CO₂, may affect litter palatability for soil fauna. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, GRASS, GROWTH, NITROGEN, ONISCUS-ASELLUS, PLANTS, RESPONSES, SOIL BIOTA

437

Cotrufo, M.F., and A. Gorissen. 1997. Elevated CO₂ enhances below-ground C allocation in three perennial grass species at different levels of N availability. *New Phytologist* 137(3):421-431.

Three perennial grass species, *Lolium perenne* L., *Agrostis capillaris* L. and *Festuca ovina* L., were homogeneously labelled in phytotrons with (CO₂)-C-14 at two CO₂ concentrations (350 and 700 $\mu\text{l l}^{-1}$). Plants were grown under two nitrogen regimes: one with a minor addition of 8 kg N ha⁻¹, the other with an addition of 278 kg N ha⁻¹. Carbon allocation over the different compartments of the plant/soil systems was measured: shoots, roots, rhizosphere soil (soil solution, microbial biomass and soil residue), and bulk soil. Elevated CO₂ increased total net C-14 recovery in all species by 14%, and significantly enhanced the below-ground C-14 allocation by 26%, this enhancement was 24%, 39% and 21%, for root, rhizosphere soil and bulk soil, respectively. Within the rhizosphere soil, the C-14 amounts in the soil solution (+ 69 %) and soil residue (+ 49 %) increased significantly. Total microbial biomass-C in the rhizosphere soil was also increased (15%) by the elevated CO₂ treatment, but only in proportion to the increased root mass. No interactions were observed between the elevated CO₂ and N treatments. The N treatment increased total net C-14 recovery by more than 300% and C-14 was preferentially allocated to the shoots, leading to a significant increase in shoot-to-root ratio. However, N fertilization also increased (+ 111 %) the absolute amount of C-14 in soil. The three species behaved differently, but no interactions were observed between CO₂ treatment and plant species. These results show that elevated CO₂ induces an increased C input into soil for all three grass species at both N levels. However, the highest absolute amounts were found in the soils of the fastest growing species and at the highest N level.

KEYWORDS: ATMOSPHERIC CO₂, BIOMASS CARBON, CARBON DIOXIDE, CO₂- ENRICHMENT, DECOMPOSITION, GROWTH, NITROGEN, RESPONSES, ROOT, SOIL SYSTEM

438

Cotrufo, M.F., and P. Ineson. 1996. Elevated CO₂ reduces field decomposition rates of *Betula pendula* (Roth) leaf litter. *Oecologia* 106(4):525-530.

The effect of elevated atmospheric CO₂ and nutrient supply on elemental composition and decomposition rates of tree leaf litter was studied using litters derived from birch (*Betula pendula* Roth.) plants grown under two levels of atmospheric CO₂ (ambient and ambient+250 ppm) and two nutrient regimes in solar domes. CO₂ and nutrient treatments affected the chemical composition of leaves, both independently and interactively. The elevated CO₂ and unfertilized soil regime significantly enhanced lignin/N and C/N ratios of birch leaves. Decomposition was studied using field litter-bags, and marked differences were observed in the decomposition rates of litters derived from the two treatments, with the highest weight remaining being associated with litter derived from the enhanced CO₂ and unfertilized regime. Highly significant correlations were shown between birch litter decomposition rates and lignin/N and C/N ratios. It can be concluded, from this study, that at levels of atmospheric CO₂ predicted for the middle of the next century a deterioration of litter quality will result in decreased decomposition rates, leading to reduction of nutrient mineralization and increased C storage in forest ecosystems. However, such conclusions are difficult to generalize, since tree responses to elevated CO₂ depend on soil nutritional status.

KEYWORDS: ATMOSPHERIC CO₂, AVAILABILITY, CARBON DIOXIDE, CASTANEA-SATIVA MILL, ENRICHMENT, LIGNIN CONTROL, NITROGEN, PLANTS, QUALITY, SEEDLINGS

439

Cotrufo, M.F., P. Ineson, and A.P. Rowland. 1994. Decomposition of tree leaf litters grown under elevated CO₂ - effect of litter quality. *Plant and Soil* 163(1):121-130.

Ash (*Fraxinus excelsior* L.), birch (*Betula pubescens* Ehrh.), sycamore

(*Acer pseudoplatanus* L.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) leaf litters were monitored for decomposition rates and nutrient release in a laboratory microcosm experiment. Litters were derived from solar domes where plants had been exposed to two different CO₂ regimes: ambient (350 μmol L⁻¹ CO₂) and enriched (600 μmol L⁻¹ CO₂). Elevated CO₂ significantly affected some of the major litter quality parameters, with lower N, higher lignin concentrations and higher ratios of C/N and lignin/N for litters derived from enriched CO₂. Respiration rates of the deciduous species were significantly decreased for litters grown under elevated CO₂, and reductions in mass loss at the end of the experiment were generally observed in litters derived from the 600 ppm CO₂ treatment. Nutrient mineralization, dissolved organic carbon, and pH in microcosm leachates did not differ significantly between the two CO₂ treatments for any of the species studied. Litter quality parameters were examined for correlations with cumulative respiration and decomposition rates: N concentration, C/N and lignin/N ratios showed the highest correlations, with differences between litter types. The results indicate that higher C storage will occur in soil as a consequence of litter quality changes resulting from higher atmospheric concentrations of CO₂.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, LIGNIN CONTROL, NITROGEN, NUTRIENT- UPTAKE, ORGANIC-MATTER, RESPONSES, SEEDLINGS, SUBSTRATE QUALITY

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Cotrufo, M.F., P. Ineson, and A. Scott. 1998. Elevated CO₂ reduces the nitrogen concentration of plant tissues. *Global Change Biology* 4(1):43-54.

We summarize the impacts of elevated CO₂ on the N concentration of plant tissues and present data to support the hypothesis that reductions in the quality of plant tissue commonly occur when plants are grown under elevated CO₂. Synthesis of existing data showed an average 14% reduction of N concentrations in plant tissue generated under elevated CO₂ regimes. However, elevated CO₂ appeared to have different effects on the N concentrations of different plant types, as the reported reductions in N have been larger in C₃ plants than in C₄ plants and N₂-fixers. Under elevated CO₂ plants changed their allocation of N between above- and below-ground components: root N concentrations were reduced by an average of 9% compared to a 14% average reduction for above-ground tissues. Although the concentration of CO₂ treatments represented a significant source of variance for plant N concentration, no consistent trends were observed between them.

KEYWORDS: ALLOCATION PATTERNS, ATMOSPHERIC CARBON-DIOXIDE, BETULA-PENDULA ROTH, CLOVER TRIFOLIUM-REPENS, INSECT PERFORMANCE, LEAF GAS- EXCHANGE, LIRIODENDRON-TULIPIFERA L, LITTER DECOMPOSITION, MINERAL NUTRITION, NUTRIENT STATUS

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Cotrufo, M.F., A. Raschi, M. Lanini, and P. Ineson. 1999. Decomposition and nutrient dynamics of *Quercus pubescens* leaf litter in a naturally enriched CO₂ Mediterranean ecosystem. *Functional Ecology* 13(3):343-351.

1. The chemical composition (i.e. N, P, C, lignin and polyphenol concentrations) of *Quercus pubescens* leaf litter derived from a natural CO₂ spring in Tuscany (Italy) was analysed and compared to litter from a nearby reference site. Litter was incubated for 25 months at both the natural CO₂ spring and the reference site, and monitored for decomposition rates, nutrient and lignin concentrations. 2. Long-term exposure to elevated CO₂ concentrations from the natural spring was associated with a change in the chemical composition of the Oak leaf

litter, with decreases in P and polyphenol concentrations and increases in lignin. No differences in N concentrations were observed between the enriched CO₂ litter from the natural spring and the reference litter. 3. Decomposition was reduced in the CO₂ spring, with the lower P concentration of the native litter, combined with the lack of soil fauna observed at that site, being the factors most probably responsible for the measured decreases in mass loss. However, litter from the CO₂ spring and reference litter decomposed at the reference site showed similar rates of decomposition. 4. All litter showed similar N concentrations during decomposition, with N being mineralized throughout the incubation period from both litter regardless of the site of incubation. In contrast, P dynamics differed between litter, with P being immobilized in the litter derived from the spring, and mineralized from the reference litter. When the litter from the spring was incubated at the reference site, there was a trend for net P uptake from the surrounding environment. The chemical composition of decomposing litter from the spring appeared to match that of the reference litter after 3 months of incubation at the reference site. 5. The results from the CO₂ spring suggest that litter decomposition may be retarded under elevated levels of atmospheric CO₂. However, results from field surveys around CO₂ vents should be viewed with caution because differences may relate to factors other than the known differences in CO₂ concentrations.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO₂, LIGNIN CONTROL, NITROGEN, QUALITY, RATES, RELEASE, SCOTS PINE FOREST, SOIL CARBON, TALLGRASS PRAIRIE

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Coughenour, M.B., and D.X. Chen. 1997. Assessment of grassland ecosystem responses to atmospheric change using linked plant-soil process models. *Ecological Applications* 7(3):802-827.

Models of photosynthesis, plant growth, and biophysical processes were linked with models that simulate water, nutrient, and carbon flows through plant-soil ecosystems. The linked ecosystem model was applied to examine ecosystem-level responses to CO₂, temperature, precipitation, and global-warming scenarios in grasslands of Colorado and Kansas, USA, and Kenya. The model predicted that increased temperatures would decrease primary production at current CO₂ levels, but decreases were reversed by doubling atmospheric CO₂ concentration. Greater increases in daily minimum temperatures than daily maximum temperatures mitigated reductions in photosynthesis and water-use efficiency (WUE) later in the day, more than offsetting increases in nighttime respiration rates under warmer temperatures. A temperature increase of 5 degrees C reduced organic carbon in grassland soils by 20-30%, through effects on plant growth and decomposition, but the doubled CO₂ negated soil carbon losses by increasing plant growth. Under higher precipitation and doubled CO₂, soil carbon stocks increased, or decreased little, in response to warmer temperatures. Doubling CO₂ increased net primary production (NPP) by 31-45% in a simulated Colorado C-4 grassland, by 20-70% in a Colorado C-3 grassland, by 23-31% in a Kansas C-4 grassland, and by 23-35% in a Kenya C-4 grassland at ambient precipitation levels. Growth was shifted belowground, thus weakening aboveground responses. Higher temperatures strengthened the positive NPP responses to CO₂. Larger positive responses to elevated CO₂ were modeled under drier conditions, and smaller responses were modeled under wetter conditions. NPP increases under elevated CO₂ were mostly caused by increased plant WUE at all sites, which was brought about by partial stomatal closure. Decreased N concentrations in plant litter under elevated CO₂ slowed N mineralization, but greater plant production and thus greater litter inputs into the soil under elevated CO₂ offset the negative effects of lower litter quality. Decreases in plant N concentration under elevated CO₂ also reduced plant N requirements. At current atmospheric CO₂ (350 μmol/mol), a general circulation model (GCM) climate-change scenario decreased NPP and soil organic matter (SOM) in Colorado but not in Kansas or Kenya. A second GCM climate-change scenario either

affected NPP and SOM little, or increased NPP and SOM at current CO₂. NPP and SOM responses in the simulated grasslands were very sensitive to precipitation, which GCMs predict with relatively low confidence. Doubled CO₂ partially or completely offset decreases in NPP and SOM under climate-change scenarios.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CLIMATE CHANGE, ELEVATED CO₂ CONCENTRATIONS, LEAF GAS- EXCHANGE, MIXED-LAYER MODEL, RISING CO₂, STOMATAL CONDUCTANCE, TALLGRASS PRAIRIE, WATER-USE

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Cournac, L., B. Dimon, P. Carrier, A. Lohou, and P. Chagvardieff. 1991. Growth and photosynthetic characteristics of *Solanum tuberosum* plantlets cultivated in vitro in different conditions of aeration, sucrose supply, and CO₂ enrichment. *Plant Physiology* 97(1):112-117.

Growth characteristics, oxygen exchange, and carbohydrate and chlorophyll contents were determined 30 days after subculturing of single node-derived plantlets of *Solanum tuberosum* cv Haig cultivated in vitro. Cultivation conditions were: (a) photomixotrophy in closed vessel, (b) photomixotrophy in closed vessel on medium supplemented with silver thiosulfate, (c) photomixotrophy in aerated vessel, (d) photoautotrophy in air, (e) photoautotrophy in CO₂-enriched air. In photomixotrophic conditions, aeration of the vessel enhanced sucrose utilization and had a positive effect on plantlet growth. In photoautotrophic conditions, growth of the plantlets was slow in air and was strongly enhanced by CO₂ enrichment of the atmosphere. Starch to sucrose ratios were higher in plants grown photoautotrophically than in plants grown with sucrose in the medium. Oxygen exchange characteristics on a chlorophyll basis were similar between the plantlets when measured under moderate light, and resembled those of greenhouse plant leaves. In high light, however, plantlets grown photoautotrophically in a CO₂-enriched atmosphere had higher oxygen exchange rates. We concluded from these results that potato plantlets in vitro in conditions (c), (d), and (e) developed C₃-plant photosynthetic characteristics, which were in photoautotrophically grown plantlets comparable to those of field-grown plants.

KEYWORDS: CARBON DIOXIDE, CULTURE, ETHYLENE, EXCHANGE, LEAVES, LIGHT, O₂, POTATO, RESPIRATION, SPECIFICITY

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Cournac, L., B. Dimon, and G. Peltier. 1993. Evidence for o-18 labeling of photorespiratory CO₂ in photoautotrophic cell-cultures of higher-plants illuminated in the presence of o-18(2). *Planta* 190(3):407-414.

The O-18-enrichment of CO₂ produced in the light or during the post-illumination burst was measured by mass spectrometry when a photoautotrophic cell suspension of *Euphorbia characias* L. was placed in photorespiratory conditions in the presence of molecular O-18(2). The only O-18-labeled species produced was (COO)-O-18-O-16; no (COO)-O-18-O-16 could be detected. Production of (COO)-O-18-O-16 ceased after addition of two inhibitors of the photosynthetic carbon-oxidation cycle, aminoxyacetate or aminoacetonitrile, and was inhibited by high levels of CO₂. The average enrichment during the post-illumination burst was estimated to be 46±15% of the enrichment of the O₂ present during the preceding light period. Addition of exogenous carbonic anhydrase, by catalyzing the exchange between CO₂ and H₂O, drastically diminished the O-18-enrichment of the produced CO₂. The very low carbonic-anhydrase level of the photoautotrophic cell suspension probably explains why the O-18 labeling of photorespiratory CO₂ could be observed for the first time. These data allow the establishment of a direct link between O₂ consumption and CO₂

production in the light, and the conclusion that CO₂ produced in the light results, at least partially, from the mitochondrial decarboxylation of the glycine pool synthesized through the photosynthetic carbon-oxidation cycle. Analysis of the (COO)-O-18-O-16 and CO₂ kinetics provides a direct and reliable way to assess in vivo the real contribution of photorespiratory metabolism to CO₂ production in the light.

KEYWORDS: INHIBITION, LEAVES, LIGHT, MASS-SPECTROMETRIC DETERMINATION, O₂, OXYGEN- EXCHANGE, PHOSPHOGLYCOLATE, PHOTORESPIRATION, PHOTOSYNTHESIS, WHEAT

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Couteaux, M.M., C. Kurz, P. Bottner, and A. Raschi. 1999. Influence of increased atmospheric CO₂ concentration on quality of plant material and litter decomposition. *Tree Physiology* 19(4-5):301-311.

Nitrogen (N) and lignin concentrations in plant tissues and litter of plants grown in greenhouses or open-top chambers in elevated atmospheric CO₂ concentration were compared with those of plants grown in ambient air in short-term studies. We also compared the N concentration of plant material of *Quercus ilex* L. and *Q. pubescens* Willd. growing in the vicinity of natural CO₂-springs with that of the same species growing at a control site. In the short-term studies, elevated CO₂ caused significant decreases in tissue N concentration and the extent of the decrease varied with species. Nitrogen amendment of the soil lessened the CO₂-enrichment effect. Lignin concentration was modified by elevated CO₂ and the effect was species specific, but no general positive or negative trend was evident. A comparison of trees growing under natural conditions near a natural CO₂-spring and at a control site revealed no site differences in N concentration of the plant material. A comparison of published results on decomposition rates of litter produced in elevated atmospheric CO₂ and in ambient air indicated that CO₂ enrichment can cause both enhancements and decreases of carbon mineralization. We conclude that (1) long-term responses to elevated CO₂ could differ from the results obtained from short-term studies and that (2) biodiversity could be an important factor altering the sign of the feedback on atmospheric CO₂ concentration. We also discuss the implications of our finding of a long-term, inhibitory effect of the initial N concentration of litter on the decomposition rate of litter and its consequence on ecosystem feedback.

KEYWORDS: BETULA-PENDULA ROTH, CARBON DIOXIDE, ELEVATED CO₂, LEAF LITTER, LIGNIN CONTROL, NITROGEN, ORGANIC-MATTER, RATES, SOIL CARBON, TERM DECOMPOSITION

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Couteaux, M.M., L.J. Monrozier, and P. Bottner. 1996. Increased atmospheric CO₂: Chemical changes in decomposing sweet chestnut (*Castanea sativa*) leaf litter incubated in microcosms under increasing food web complexity. *Oikos* 76(3):553-563.

Increased concentrations of atmospheric CO₂ induced a lower nitrogen concentration in sweet chestnut litter. The C:N ratio was about 35 at a 350 μmol l⁻¹ CO₂ concentration and about 70 at 700 μmol l⁻¹. The CO₂ enrichment increased the proportion of hemicelluloses and cellulose and decreased the proportion of lignin. Both litters were decomposed in microcosms with animal food webs of different complexities. The chemical composition of the decomposed litter (nitrogen, water-soluble compounds, cellulose, hemicelluloses and lignin) was related to the initial composition and to the mass loss. Rates of hemicelluloses and lignin decomposition and nitrogen dynamics were the most affected by the change in litter quality due to atmospheric CO₂ enrichment. In N-rich litter, hemicelluloses were almost completely decomposed and lignin remained intact without effect of animal grazing.

In N-poor litter derived from CO₂-enriched atmosphere, increased complexity of invertebrate food webs significantly enhanced decomposition of all the chemical components. By adding different groups of animals, some limiting factors were overcome and new substrates were liberated for microbial decomposition. It was hypothesized that the decomposition process was controlled by the interaction between lignin and nitrogen.

KEYWORDS: DYNAMICS, ELEVATED CO₂, FOREST, LIGNIN CONTROL, LONG-TERM DECOMPOSITION, MASS-LOSS, NITROGEN, PINE NEEDLE LITTER, SOIL, SUBSTRATE QUALITY

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Couteaux, M.M., M. Mousseau, M.L. Celerier, and P. Bottner. 1991. Increased atmospheric CO₂ and litter quality - decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos* 61(1):54-64.

Two-year-old chestnut trees were grown for two yr under ambient (350 ppm) and enriched (700 ppm) CO₂ concentrations, in two naturally lit growth chambers. The doubling of CO₂ resulted in a dilution of the nitrogen concentration in the leaf litter, with C:N ratios of 40 and 75 for the ambient and enriched CO₂ concentrations, respectively. The litter was sterilized and inoculated with microflora and animal groups of increasing complexity (microflora + Protozoa; + nematodes; + Collembola; + Isopoda) and incubated over 24 wk. Every two wk, the CO₂ release was measured and the litter was leached with demineralized H₂O. The following analyses were performed on the leachates: pH, total nitrogen, dissolved and particulate carbon, inorganic nitrogen (NH₄⁺ and NO₃⁻), phosphate, and biological counts (Protozoa, nematodes and Rotifera). The initial decomposition stages (the first 12 wk) were dominated by the litter quality factor: CO₂ release and nitrogen losses in leachates were higher and carbon losses lower in water leaching from the litter with low C:N ratio. Towards the late stages, when carbon mineralization decreased in the control litter, the animal effect emerged in litter with a high C:N ratio. Two groups appeared: (1) In the microflora + Protozoa units, carbon mineralization was reduced by 60% compared with the control litter. (2) In the diversified food web combinations, it became progressively higher with increasing complexity of the animal community and was enhanced by 30% compared with the control litter. This unexpected fundamental difference was explained by a change in the composition and activity of the microflora. Litter bleaching, respiration, C and N leaching and acidification rose with increasing animal complexity of the systems. Biological and chemical reasons explaining the invasion by white-rot fungi and its activity only in the material with a high C:N ratio are discussed. During the 24 wk, nitrogen and phosphorus mineralization was very low, indicating a high incorporation of the nutrient in the soil biomass.

KEYWORDS: BREAKDOWN, CARBON, CASTANEA-SATIVA MILL, DECIDUOUS WOODLAND SOILS, FAUNA, LIGNIN CONTROL, MINERALIZATION, NITROGEN, RAW HUMUS, WEIGHT-LOSS

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Coviella, C.E., and J.T. Trumble. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology* 13(4):700-712.

In the enriched carbon dioxide atmosphere expected in the next century, many species of herbivorous insects will confront less nutritious host plants that will induce both lengthened larval developmental times and greater mortality. The limited data currently available suggest that the effect of increased atmospheric CO₂ on herbivory will be not only highly species-specific but also specific to each insect-plant system. Several scenarios can be predicted however. (1) local extinctions will occur; (2) the endangered species status as well as the pest status of

some insect species will change; (3) geographic distributions for some insect species will shift with host-plant ranges; and (4) changes in the population dynamics of affected insect species will influence their interactions with other insects and plants. For insect conservation purposes, it is critical to begin long-term studies on the effects of enhanced CO₂ levels on insect populations. An analysis of the available literature indicates that many orders containing insect species important for ecosystem conservation, and even those important as agricultural or medical pests, have not been examined. Without a major increase in research on this topic, we will be unprepared for the species changes that will occur, we will lose the opportunity to document just how some insects adapt to elevated CO₂ levels, and we will lack the information necessary for effective conservation efforts.

KEYWORDS: CACTOBLASTIS-CACTORUM, CLIMATE CHANGE, CORN-ROOTWORM COLEOPTERA, ENRICHED CO₂ ATMOSPHERES, GYPSY-MOTH, HERBIVORE INTERACTIONS, LOBLOLLY-PINE, SECONDARY METABOLITES, SOUR ORANGE TREES, SPODOPTERA-EXIGUA

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Cowling, S.A. 1999. Simulated effects of low atmospheric CO₂ on structure and composition of North American vegetation at the Last Glacial Maximum. *Global Ecology and Biogeography* 8(2):81-93.

1. Physiological experiments have indicated that the lower CO₂ levels of the last glaciation (200 μmol mol⁻¹) probably reduced plant water-use efficiency (WUE) and that they combined with increased aridity and colder temperatures to alter vegetation structure and composition at the Last Glacial Maximum (LGM). 2. The effects of low CO₂ on vegetation structure were investigated using BIOME3 simulations of leaf area index (LAI), and a two-by-two factorial experimental design (modern/LGM CO₂, modern/ LGM climate). 3. Using BIOME3, and a combination of lowered CO₂ and simulated LGM climate (from the NCAR-CCM1 model), results in the introduction of additional xeric vegetation types between open woodland and closed-canopy forest along a latitudinal gradient in eastern North America. 4. The simulated LAI of LGM vegetation was 25- 60% lower in many regions of central and eastern United States relative to modern climate, indicating that glacial vegetation was much more open than today. 5. Comparison of factorial simulations show that low atmospheric CO₂ has the potential to alter vegetation structure (LAI) to a greater extent than LGM climate. 6. If the magnitude of LAI reductions simulated for glacial North America were global, then low atmospheric CO₂ may have promoted atmospheric warming and increased aridity, through alteration of rates of water and heat exchange with the atmosphere.

KEYWORDS: C-4 ANNUALS, CARBON ISOTOPE DISCRIMINATION, CLIMATE CHANGE, ELEVATED CO₂, FOREST ECOSYSTEMS, GENERAL-CIRCULATION MODEL, ICE CORE, LEAF-AREA INDEX, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

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Cowling, S.A., and R.F. Sage. 1998. Interactive effects of low atmospheric CO₂ and elevated temperature on growth, photosynthesis and respiration in *Phaseolus vulgaris*. *Plant, Cell and Environment* 21(4):427-435.

For most of the past 250 000 years, atmospheric CO₂ has been 30-50% lower than the current level of 360 μmol CO₂ mol⁻¹ air. Although the effects of CO₂ on plant performance are well recognized, the effects of low CO₂ in combination with abiotic stress remain poorly understood. In this study, a growth chamber experiment using a two-by-two factorial design of CO₂ (380 μmol mol⁻¹, 200 μmol mol⁻¹) and temperature (25/20 degrees C day/night, 36/29 degrees C) was conducted to evaluate the interactive effects of CO₂ and temperature

variation on growth, tissue chemistry and leaf gas exchange of *Phaseolus vulgaris*. Relative to plants grown at 380 pmol mol⁻¹ and 25/20 degrees C, whole plant biomass was 36% less at 380 mu mol mol⁻¹ x 36/29 degrees C, and 37% less at 200 mu mol mol⁻¹ x 25/20 degrees C. Most significantly, growth at 200 mu mol mol⁻¹ x 36/29 degrees C resulted in 77% less biomass relative to plants grown at 380 pmol mol⁻¹ x 25/20 degrees C. The net CO₂ assimilation rate of leaves grown in 200 mu mol mol⁻¹ x 25/20 degrees C was 40% lower than in leaves from 380 pmol mol⁻¹ x 25/20 degrees C, but similar to leaves in 200 mu mol mol⁻¹ x 36/29 degrees C. The leaves produced in low CO₂ and high temperature respired at a rate that was double that of leaves from the 380 mu mol mol⁻¹ x 25/20 degrees C treatment. Despite this, there was little evidence that leaves at low CO₂ and high temperature were carbohydrate deficient, because soluble sugars, starch and total non-structural carbohydrates of leaves from the 200 mu mol mol⁻¹ x 36/29 degrees C treatment were not significantly different in leaves from the 380 mu mol mol⁻¹ x 25/20 degrees C treatment. Similarly, there was no significant difference in percentage root carbon, leaf chlorophyll and leaf/root nitrogen between the low CO₂ x high temperature treatment and ambient CO₂ controls. Decreased plant growth was correlated with neither leaf gas exchange nor tissue chemistry. Rather, leaf and root growth were the most affected responses, declining in equivalent proportions as total biomass production. Because of this close association, the mechanisms controlling leaf and root growth appear to have the greatest control over the response to heat stress and CO₂ reduction in *P. vulgaris*.

KEYWORDS: ACCLIMATION, ALLOCATION, BIOCHEMISTRY, C-4 ANNUALS, CARBON DIOXIDE, GAS-EXCHANGE, LEAF RESPIRATION, LEAVES, PLANTS, SENESCENCE

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Cowling, S.A., and M.T. Sykes. 1999. Physiological significance of low atmospheric CO₂ for plant- climate interactions. *Quaternary Research* 52(2):237-242.

Methods of palaeoclimate reconstruction from pollen are built upon the assumption that plant-climate interactions remain the same through time or that these interactions are independent of changes in atmospheric CO₂. The latter may be problematic because air trapped in polar ice caps indicates that atmospheric CO₂ has fluctuated significantly over at least the past 400,000 yr, and likely the last 1.6 million yr. Three other points indicate potential biases for vegetation-based climate proxies. First, C-3-plant physiological research shows that the processes that determine growth optima in plants (photosynthesis, mitochondrial respiration, photorespiration) are all highly CO₂-dependent, and thus were likely affected by the lower CO₂ levels of the last glacial maximum. Second, the ratio of carbon assimilation per unit transpiration (called water-use efficiency) is sensitive to changes in atmospheric CO₂ through effects on stomatal conductance and may have altered C-3-plant responses to drought. Third, leaf gas- exchange experiments indicate that the response of plants to carbon-depleting environmental stresses are strengthened under low CO₂ relative to today. This paper reviews the scope of research addressing the consequences of low atmospheric CO₂ for plant and ecosystem processes and highlights why consideration of the physiological effects of low atmospheric CO₂ on plant function is recommended for any future refinements to pollen- based palaeoclimatic reconstructions. (C) 1999 University of Washington.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, DIOXIDE STARVATION, ECOSYSTEMS, ELEVATED CO₂, LAST GLACIAL MAXIMUM, PHASEOLUS-VULGARIS, PHOTOSYNTHESIS, POLLEN, VEGETATION, WATER-USE EFFICIENCY

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Cox, P.M., R.A. Betts, C.B. Bunton, R.L.H. Essery, P.R. Rowntree,

and J. Smith. 1999. The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. *Climate Dynamics* 15(3):183-203.

Recent improvements to the Hadley Centre climate model include the introduction of a new land surface scheme called "MOSES" (Met Office Surface Exchange Scheme). MOSES is built on the previous scheme, but incorporates in addition an interactive plant photosynthesis and conductance module, and a new soil thermodynamics scheme which simulates the freezing and melting of soil water, and takes account of the dependence of soil thermal characteristics on the frozen and unfrozen components. The impact of these new features is demonstrated by comparing 1 x CO₂ and 2 x CO₂ climate simulations carried out using the old (UKMO) and new (MOSES) land surface schemes. MOSES is found to improve the simulation of current climate. Soil water freezing tends to warm the high-latitude land in the northern Hemisphere during autumn and winter, whilst the increased soil water availability in MOSES alleviates a spurious summer drying in the mid-latitudes. The interactive canopy conductance responds directly to CO₂, suppressing transpiration as the concentration increases and producing a significant enhancement of the warming due to the radiative effects of CO₂ alone.

KEYWORDS: GENERAL-CIRCULATION MODELS, INCREASED CO₂, PARAMETRIZATION, PHOTOSYNTHESIS, PROJECT, SCALE, SCHEMES, SOILS, STOMATAL CONDUCTANCE, TRANSPIRATION

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Craig, S.G., and K.J. Holmen. 1995. Uncertainties in future CO₂ projections. *Global Biogeochemical Cycles* 9(1):139-152.

The perceived budget imbalance in the global carbon cycle has been suggested to result from, among other processes, CO₂ fertilization of the terrestrial biosphere and/or enhanced regrowth of previously felled temperate forest. These two processes are incorporated into a box diffusion model of the ocean-atmosphere system coupled to a five-box terrestrial biosphere. The extent to which historical fossil fuel and land use change emission data can be reconciled with the observed atmospheric CO₂ concentration record is examined. Furthermore, the sensitivity of future CO₂ projections to the nature of the budget imbalance is investigated. It is found that the CO₂ record can accommodate a carbon budget balanced by CO₂ fertilization but that the balance with forest regrowth is more difficult. Future CO₂ projections are found to be sensitive to how the carbon budget is balanced, even relative to uncertainties in future emissions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CYCLE, DIFFUSION-MODEL, EMISSIONS, FORESTS, FOSSIL-FUELS, PAST 2 CENTURIES, SINKS, STORAGE

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Cramer, M.D., Z.F. Gao, and S.H. Lips. 1999. The influence of dissolved inorganic carbon in the rhizosphere on carbon and nitrogen metabolism in salinity-treated tomato plants. *New Phytologist* 142(3):441-450.

The influence of variation in the concentration of dissolved inorganic carbon (DIC) in the form of CO₂ and HCO₃⁻ in the root media on the C and N metabolism of *Lycopersicon esculentum* cv. F144 was investigated under both saline and non-saline conditions. Tomato seedlings were grown in hydroponic culture (pH 6.5) with or without NaCl, and the root solution was aerated with either ambient CO₂ (360 mol mol⁻¹) or CO₂- enriched air (5000 mu mol mol⁻¹). Nitrate uptake and root tissue NO₃⁻ concentrations were increased slightly by elevated rhizosphere DIC concentrations in both control and salinity-treated plants. This is associated with 46% higher nitrate reductase activity in the roots of control plants supplied with elevated DIC than in

those supplied with ambient DIG. The activity of phosphoenolpyruvate carboxylase (PEPc) in vitro in control and salinity-treated plants was unaffected by the supply of elevated rhizosphere DIC concentrations. However, PEPc activity in vitro was considerably higher than the rates of PEPc activity in vivo reported previously, indicating that PEPc activity was not in itself a limitation on the provision of anaplerotic C. Therefore elevated DIC concentration in the rhizosphere stimulated the uptake of NO₃⁻ and provided alternative C skeletons for the assimilation of the NH₄⁺ resulting from NO₃⁻ reduction into amino acids within the roots. Salinity stimulated root glutamine synthetase (GS) activity up to double that in control plants. Furthermore, elevated DIC caused an increase in leaf and root GS activity of control plants while inhibiting GS activity in the roots of salinity-treated plants. Glutamine:2-oxoglutarate aminotransferase (GOGAT) activity of salinity-treated plants was doubled by elevated rhizosphere DIC concentrations. These changes in GS and GOGAT activity must reflect changes in amino acid synthesis. Under saline conditions the xylem transport of NO₃⁻ is partly blocked and a larger root assimilation develops, requiring not only the transamination of 2-oxoglutarate to glutamate but also that of oxaloacetate to aspartate and the transamidation of aspartate to asparagine.

KEYWORDS: AMMONIUM NUTRITION, ANHYDRASE ACTIVITY, ASSIMILATION, BARLEY, CO₂, FIXATION, NITRATE REDUCTASE, PHOSPHOENOLPYRUVATE CARBOXYLASE, ROOTS, SEEDLINGS

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Cramer, M.D., and S.H. Lips. 1995. Enriched rhizosphere CO₂ concentrations can ameliorate the influence of salinity on hydroponically grown tomato plants. *Physiologia Plantarum* 94(3):425-432.

Our previous work indicated that salinity caused a shift in the predominant site of nitrate reduction and assimilation from the shoot to the root in tomato plants. In the present work we tested whether an enhanced supply of dissolved inorganic carbon (DIC, CO₂ + HCO₃⁻) to the root solution could increase anaplerotic provision of carbon compounds for the increased nitrogen assimilation in the root of salinity-stressed *Lycopersicon esculentum* (L.) Mill. cv. F144. The seedlings were grown in hydroponic culture with 0 or 100 mM NaCl and aeration of the root solution with either ambient or CO₂-enriched air (5 000 μmol mol⁻¹). The salinity-treated plants accumulated more dry weight and higher total N when the roots were supplied with CO₂-enriched aeration than when aerated with ambient air. Plants grown with salinity and enriched DIC also had higher rates of NO₃⁻ uptake and translocated more NO₃⁻ and reduced N in the xylem sap than did equivalent plants grown with ambient DIC. Incorporation of DIC was measured by supplying a 1-h pulse of (HCO₃⁻)-C-14 to the roots followed by extraction with 80% ethanol. Enriched DIC increased root incorporation of DIC 10- fold in both salinized and non-salinized plants. In salinity-stressed plants, the products of dissolved inorganic C-14 were preferentially diverted into amino acid synthesis to a greater extent than in non-salinized plants in which label was accumulated in organic acids. It was concluded that enriched DIC can increase the supply of N and anaplerotic carbon for amino acid synthesis in roots of salinized plants. Thus enriched DIC could relieve the limitation of carbon supply for ammonium assimilation and thus ameliorate the influence of salinity on NO₃⁻ uptake and assimilation as well as on plant growth.

KEYWORDS: AMMONIUM, INORGANIC CARBON, METABOLISM, NITRATE ASSIMILATION, NITROGEN, NUTRITION, REDUCTION, ROOTS, SEEDLINGS, SHOOT

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Cramer, M.D., and S.H. Lips. 1995. The influence of enriched root-zone CO₂ concentrations on growth, nitrogen metabolism and root HCO₃⁻ incorporation in salinity stressed *Lycopersicon esculentum*. *Acta*

Phytopathologica Et Entomologica Hungarica 30(1-2):105-118.

Tomato plants grown with salinity reduce/assimilate a larger proportion of NO₃⁻ taken up in the roots than do non-salinized plants. We investigated whether enriched CO₂ in the root solution could increase anaplerotic provision of carbon for root nitrogen assimilation in salinity stressed plants. Tomato seedlings were grown in hydroponic culture with and without 100 mM NaCl and with aeration of the root solution with either ambient or CO₂ enriched air (5000 μmol mol⁻¹). The salinity treated plants accumulated more dry weight and higher total N when the roots were supplied with CO₂ enriched aeration than when aerated with ambient air. Concentrations of K⁺ in the leaves and roots were higher in plants treated with enriched CO₂. Enriched root-zone CO₂ increased root incorporation of dissolved inorganic carbon (DIC). In salinity stressed plants the products of (DIC)-C-14 were diverted into amino acid synthesis to a greater extent than in non-salinized plants. It was concluded that enriched root-zone DIC could provide an increased anaplerotic source of carbon for amino acid synthesis in roots, partially ameliorating the influence of salinity on plant growth.

KEYWORDS: AMMONIUM, CARBON DIOXIDE, LEAF RESPIRATION, NITRATE ASSIMILATION, NUTRITION, PLANTS, REDUCTION, RESPONSES, SHOOT

457

Cramer, M.D., and M.B. Richards. 1999. The effect of rhizosphere dissolved inorganic carbon on gas exchange characteristics and growth rates of tomato seedlings. *Journal of Experimental Botany* 50(330):79-87.

The possibility that an enhanced supply of dissolved inorganic carbon (DIC = CO₂ + HCO₃⁻) to the root solution could increase the growth of *Lycopersicon esculentum* (L.) Mill. cv. F144 was investigated under both saline and non-saline root medium conditions. Tomato seedlings were grown in hydroponic culture with and without NaCl and the root solution was aerated with CO₂ concentrations in the range between 0 and 5000 μmol mol⁻¹. The biomass of both control and salinity-stressed plants grown at high temperatures (daily maximum of 37 degrees C) and an irradiance of 1500 μmol m⁻² s⁻¹ was increased by up to 200% by enriched rhizosphere DIC. The growth rates of plants grown with irradiances of less than 1000 μmol m⁻² s⁻¹ were increased by elevated rhizosphere DIC concentrations only when grown at high shoot temperatures (35 degrees C) or with salinity (28 degrees C). At high light intensities, the photosynthetic rate, the CO₂ and light-saturated photosynthetic rate (J(max)) and the stomatal conductance of plants grown at high light intensity were lower in plants supplied with enriched compared to ambient DIC. This was interpreted as 'down-regulation' of the photosynthetic system in plants supplied with elevated DIC. Labelled organic carbon in the xylem sap derived from root (DIC)-C-14 incorporation was found to be sufficient to deliver carbon to the shoot at rates equivalent to 1% and 10% of the photosynthetic rate of the plants supplied with ambient- and enriched-DIC, respectively. It was concluded that organic carbon derived from DIC incorporation and translocated in the xylem from the root to the shoot may provide a source of carbon for the shoots, especially under conditions where low stomatal conductance may be advantageous, such as salinity stress, high shoot temperatures and high light intensities.

KEYWORDS: AMMONIUM NUTRITION, ASSIMILATION, BARLEY, CO₂, METABOLISM, NITRATE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PLANTS, ROOTS, SALINITY

458

Cramer, M.D., N.A. Savidov, and S.H. Lips. 1996. The influence of enriched rhizosphere CO₂ on N uptake and metabolism in wild-type and NR-deficient barley plants. *Physiologia Plantarum* 97(1):47-54.

Positive influences of high concentrations of dissolved inorganic carbon (DIC) in the growth medium of salinity-stressed plants are associated with carbon assimilation through phosphoenolpyruvate carboxylase (PEPc) activity in roots; and also in salinity-stressed tomato plants, enriched CO₂ in the rhizosphere increases NO₃(-)-uptake. In the present study, wild-type and nitrate reductase-deficient plants of barley (*Hordeum vulgare* L. cv. Steptoe) were used to determine whether the influence of enriched CO₂ on NO₃(-)-uptake and metabolism is dependent on the activity of nitrate reductase (NR) in the plant. Plants grown in NH₄⁺ and aerated with ambient air, were transferred to either NO₃⁻ or NH₄⁺ solutions and aerated with air containing between 0 and 6500 $\mu\text{mol mol}^{-1}$ CO₂. Nitrogen uptake and tissue concentrations of NO₃⁻ and NH₄⁺ were measured as well as activities of NR and PEPc. The uptake of NO₃⁻ by the wild-type was increased by increasing CO₂. This was associated with increased *in vitro* NR activity, but increased uptake of NO₃⁻ was found also in the NR-deficient genotype when exposed to high CO₂ concentrations; so that the influence of CO₂ on NO₃⁻ uptake was independent of the reduction of NO₃⁻ and assimilation into amino acids. The increase in uptake of NO₃⁻ in wild-type plants with enriched CO₂ was the same at pH 7 as at pH 5, indicating that the relative abundance of HCO₃⁻ or CO₂ in the medium did not influence NO₃⁻ uptake. Uptake of NH₄⁺ was decreased by enriched CO₂ in a pH (5 or 7) independent fashion. Thus NO₃⁻ and NH₄⁺ uptakes are influenced by the CO₂ component of DIC independently of anaplerotic carbon provision for amino acid synthesis, and CO₂ may directly affect the uptake of NO₃⁻ and NH₄⁺ in ways unrelated to the NR activity in the tissue.

KEYWORDS: AMMONIUM NUTRITION, INORGANIC CARBON, MAIZE ROOTS, NH₄, NITRATE ASSIMILATION, NO₃, PHOSPHOENOLPYRUVATE CARBOXYLASE, SHOOT

459

Crick, S.G., and R. McConchie. 1999. Ethanol vapour reduces leaf blackening in cut flower *Protea* 'Pink Ice' stems. *Postharvest Biology and Technology* 17(3):227-231.

The effect of ethanol vapour on postharvest leaf blackening of *Protea susannae* X *compacta* 'Pink Ice' stems stored in plastic bags under darkness at 20 degrees C (+/- 1 degrees C) was assessed over a 19 day period. Application of ethanol vapour to the stems significantly reduced leaf blackening. Stems exposed to 5.6 g ethanol kg⁻¹ stem weight, had the least amount of leaf blackening with less than 20% of leaves blackened by day 14. In contrast, the control stems had 50% of leaves blackened by day 9, and 100% by day 15. The highest ethanol treatment at 11.2 g ethanol kg⁻¹ stem weight caused substantial blackening within the first 24 h of the treatment being applied. Ethanol vapour concentrations in the bag head space decreased rapidly in comparison with the bags with no stems, suggesting that ethanol was rapidly taken up by the stems. Only the highest ethanol treatment had detectable levels of ethanol in the bags after 17 days, and ethanol vapour had no effect on CO₂ concentration in the bag head space. Carbon dioxide concentrations ranged between 1.0 and 2.5%. The rate of leaf blackening on the bagged stems without ethanol was significantly less than on stems not in bags, suggesting that elevated CO₂ levels may have contributed to reduced blackening. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: FRUIT, NERIIFOLIA R

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Crookshanks, M., G. Taylor, and M. Broadmeadow. 1998. Elevated CO₂ and tree root growth: contrasting responses in *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris*. *New Phytologist* 138(2):241-250.

Root growth and respiration in elevated CO₂ (700 $\mu\text{mol mol}^{-1}$) was studied in three tree species, *Fraxinus excelsior* L., *Quercus petraea* L.

and *Pinus sylvestris* L. grown in open-top chambers (OTCs) during a long-term exposure (20 months), during which root systems were allowed to develop without restriction imposed by pots. Root growth, measured as root length using root in-growth bags was increased significantly in trees exposed to elevated CO₂, although the magnitude of the response differed considerably between species and with time of sampling, the greatest effect observed after 6 months in ash (ratio of elevated:ambient, e:a; 3.40) and the smallest effect observed in oak (e:a; 1.95). This was accompanied by changes in specific root length, with a significant decrease in all species after 6 months, suggesting that root diameter or root density were increased in elevated CO₂. Increases in root length might have resulted from an acceleration in root cell expansion, since epidermal cell size was significantly increased in the zone of elongation in ash root tips (P < 0.05). Contrasting effects of elevated CO₂ were observed for root carbohydrates, with significant increases in soluble sugars for all species (P < 0.05), but both increases and decreases in starch content were observed, depending on species, and producing a significant interaction between species and CO₂ (P < 0.001). Exposure to elevated CO₂ increased the total root d. wt for whole trees of all three species after 8 months of exposure, although the magnitude of this effect, in contrast to the root in-growth study, was greatest in Scots pine and smallest in ash. No significant effect of elevated CO₂ was observed on the root:shoot ratio. Further detailed analysis of whole root systems after 20 months confirmed that species differences in root responses to elevated CO₂ were apparent, with increased coarse and fine root production in elevated CO₂ for Scots pine and ash respectively. Lateral root number was increased in elevated CO₂ for all species, as was mean root diameter. Root respiration rates were significantly reduced in elevated CO₂ for all three species. These results provide firm evidence that exposure of trees to future CO₂ concentrations will have large effects on root system development, growth, carbohydrate status and respiration. The magnitude and direction of such effects will differ, depending on species. The consequences of such responses for the three species studied are discussed.

KEYWORDS: ARCHITECTURE, ATMOSPHERIC CARBON-DIOXIDE, EFFICIENCY, ENRICHMENT, HYBRID POPLAR, PLANT, RESPIRATION, SOIL, TEMPERATURE, WATER-USE

461

Crookshanks, M., G. Taylor, and L. Dolan. 1998. A model system to study the effects of elevated CO₂ on the developmental physiology of roots: the use of *Arabidopsis thaliana*. *Journal of Experimental Botany* 49(320):593-597.

Three developmental changes were observed in the roots of *Arabidopsis thaliana* (Columbia) when shoots were exposed to elevated CO₂. (i) The allometric coefficient, k, was enhanced significantly (P<0.001), (ii) primary root length and root extension rate were enhanced (P<0.001), Accelerated cortical cell expansion contributed to this effect and was associated with increased cell wall extensibility, measured as % plasticity. (iii) Lateral root formation and extension were also increased in elevated CO₂ (P<0.05). These results illustrate that root growth and structure was altered following exposure to elevated CO₂. The changes observed suggest that *Arabidopsis* provides a useful model which should, in future, be amenable to study using appropriate mutants allowing the genetic basis of the responses to be identified.

KEYWORDS: CELLULAR MECHANISMS, ENRICHMENT, EXPANSION, GROWTH, MUTANTS, RESPONSES

462

Crosson, P.R., and N.J. Rosenberg. 1993. An overview of the mink study. *Climatic Change* 24(1-2):159-173.

Highlights of the previous papers in this series are reviewed. Methodology developed for the MINK study has improved the ability of impacts analysis to deal with questions of (1) spatial and temporal variability in climate change; (2) CO₂- enrichment effects; (3) the reactions of complex enterprises (farms and forests) to climate change and their ability to adjust and adapt; and (4) integrated effects on current and, more particularly, on future regional economies. The methodology also provides for systematic study of adjustment and adaptation opportunities and of the inter-industry linkages that determine what the overall impacts on the regional economy might be. The analysis shows that with a 1930s 'dust bowl' climate the region-wide economic impacts would be small, after adjustments in affected sectors. In this final paper we consider whether synergistic effects among sectoral impacts and more severe climate change scenarios might alter this conclusion. The MINK analysis, as is, leads to the conclusion that a strong research capacity will be required to ensure that technologies facilitating adaptation to climate change will be available when needed. The capacity to deal with climate change also requires an open economy allowing for free trade and movement of people and for institutions that protect unpriced environmental values. More severe climate scenarios and negative synergisms can only strengthen these conclusions.

463

Crowley, T.J., and S.K. Baum. 1997. Effect of vegetation on an ice-age climate model simulation. *Journal of Geophysical Research-Atmospheres* 102(D14):16463-16480.

A growing number of studies suggest that vegetation changes can significantly influence regional climate variations. Herein we utilize a climate model (GENESIS) with a land surface vegetation package to evaluate the potential role of the very large vegetation changes that occurred during the last glacial maximum (LGM). In particular, we focus on the potential response to a significant reduction in the area of tropical rainforest. Simulations employed a global vegetation reconstruction for the LGM and Climate/Long-Range Investigation, Mapping and Prediction (CLIMAP) sea surface temperature (SST) estimates. Results indicate that expansion of dryland vegetation causes a 15-30% additional LGM cooling for Australia (0.4 degrees C) and Africa (0.9 degrees C), respectively. Turnover from conifer to tundra also causes cooling of 2 degrees-4 degrees C or more in western Europe and Siberia. However, for the largest rainforest area (Amazon Basin), inclusion of realistic vegetation increased modeled temperatures 2 degrees-4 degrees C and decreased precipitation by 10-35%. These latter results are similar to those obtained with sensitivity experiments of the effects of future Amazon deforestation. Initial assessment of the potential effect of decreased stomatal resistance due to lower ice age CO₂ levels indicates little significant response to this effect. Comparison of model-predicted low-elevation LGM temperature changes with estimates from proxy data indicate that inclusion of realistic vegetation estimates for the LGM results in slightly more than 50% agreement between models and data for low-elevation sites in low-mid latitudes. Data at variance with model predictions would appear to be explainable by considering additional changes in vegetation, ice age dust, or a 1 degree- 2 degrees C cooling below CLIMAP values. This conclusion is at variance with a 3 degree-4 degrees C tropical cooling suggested by some studies for explaining estimated land temperature changes during the LGM. In some western European sites model temperatures are colder than proxy data by 2 degrees-8 degrees C. This model-data discrepancy may be explained by less sea ice in the subpolar North Atlantic than stipulated by CLIMAP, a conclusion consistent with new marine data from that region.

KEYWORDS: BOUNDARY-CONDITIONS, EURASIAN SNOW COVER, GENERAL-CIRCULATION MODELS, GLOBAL CLIMATE, LAST GLACIAL MAXIMUM, LATE QUATERNARY, SEA-SURFACE TEMPERATURE, STOMATAL-RESISTANCE, TERRESTRIAL CARBON STORAGE, TRANSFER SCHEME LSX

464

Crush, J.R. 1993. Hydrogen evolution from root-nodules of trifolium-repens and medicago-sativa plants grown under elevated atmospheric co₂. *New Zealand Journal of Agricultural Research* 36(2):177-183.

Nitrogenase activity and hydrogen (H₂) evolution from nodules of *Trifolium repens* L. and *Medicago sativa* L. were measured on plants grown under 700 or 350 µl/l atmospheric CO₂ and day/night temperatures of 18/13-degrees-C or 28/23-degrees-C. Assays were done after 39, 47, and 54 days' exposure to the treatments. In *Trifolium*, nitrogenase activity/plant was stimulated by elevated CO₂ and higher temperatures but in *Medicago* only temperature had an effect. Hydrogen emission/plant was greater in *Trifolium* plants grown at 700 µl/l CO₂ than in plants at 350 µl/l CO₂, but in *Medicago*, H₂ emission rates did not respond to elevated CO₂. Elevated CO₂ reduced nodule relative efficiency (RE) in 39-day-old *Trifolium* plants growing at 18/13-degrees-C, but not under other conditions. It is concluded that predicted future CO₂ concentration will lead to a greater contribution from legume nitrogen (N) fixation to global H₂ sources. The magnitude of the increase will be influenced by the legume species involved and temperature.

KEYWORDS: ECONOMY, EFFICIENCY, LEGUME, MOLECULAR-HYDROGEN, NITROGEN-FIXATION, REDUCTION, RHIZOBIA, WHITE CLOVER

465

Crush, J.R. 1994. Elevated atmospheric co₂ concentration and rhizosphere nitrogen-fixation in 4 forage plants. *New Zealand Journal of Agricultural Research* 37(4):455-463.

Lolium x boucheanum (2n and 4n), *Plantago lanceolata*, and *Pennisetum clandestinum* were grown in pots of soil in growth rooms with factorial combinations of 350 or 700 µl/l atmospheric CO₂ and day/night temperatures of 28/23-degrees-C or 18/13-degrees-C. Both cultivars of *Lolium* and *P. lanceolata* grew faster with elevated CO₂ but *P. clandestinum* was unaffected. Rhizosphere nitrogenase activity, assessed by acetylene reduction, was reduced by the 700 µl/l CO₂ treatment in the tetraploid *Lolium* but otherwise did not vary significantly with CO₂ level.

KEYWORDS: ACETYLENE-REDUCTION ASSAY, ASSOCIATION, CARBON, CEREALS, GRASSES, GRASSLAND, GROWTH, ROOTS, SPECIFICITY, TRIFOLIUM-REPENS

466

Cruz, C., S.H. Lips, and M.A. Martinsloucao. 1993. The effect of nitrogen-source on photosynthesis of carob at high co₂ concentrations. *Physiologia Plantarum* 89(3):552-556.

Carob seedlings (*Ceratonia siliqua* L. cv. *Mulata*), fed with nitrate or ammonium, were grown in growth chambers containing two levels of CO₂ (360 or 800 µl l⁻¹), three root temperatures (15, 20 or 25 degrees C), and the same shoot temperature (20/24 degrees C, night/day temperature). The response of the plants to CO₂ enrichment was affected by environmental factors such as the type of inorganic nitrogen in the medium and root temperature. Increasing root temperature enhanced photosynthesis rate more in the presence of nitrate than in the presence of ammonium. Differences in photosynthetic products were also observed between nitrate- and ammonium-fed carob seedlings. Nitrate-grown plants showed an enhanced content of sucrose, while ammonium led to enhanced storage of starch. Increase in root temperature caused an increase in dry mass of the plants of similar proportions in both nitrogen sources. The enhancement of the rates of photosynthesis by CO₂ enrichment was proportionally much larger than the resulting increases

in dry mass production when nitrate was the nitrogen source. Ammonium was the preferred nitrogen source for carob at both ambient and high CO₂ concentrations. The level of photosynthesis of a plant is limited not only by atmospheric CO₂ concentration but also by the nutritional and environmental conditions of the root.

KEYWORDS: AMMONIUM, CELLS, LEAVES, PLANTS

467

Cruz, C., S.H. Lips, and M.A. Martins-Loucao. 1997. Changes in the morphology of roots and leaves of carob seedlings induced by nitrogen source and atmospheric carbon dioxide. *Annals of Botany* 80(6):817-823.

Carob seedlings were grown hydroponically for 9 weeks under 360 and 800 $\mu\text{mol mol}^{-1}$ CO₂. One of two nitrogen sources, nitrate or ammonium, was added to the nutrient medium at concentrations of 3 mol m^{-3} . Root systems of the developing plants supplied with nitrate compared to those supplied with ammonium were characterized by: (a) more biomass on the lower part of the root; (b) fewer lateral roots of first and second order; (c) longer roots; (d) higher specific root length; (e) a smaller root diameter. The morphology of the root systems of nitrate-fed plants changed in the presence of elevated carbon dioxide concentrations, resembling, more closely, that of ammonium-fed plants. Total leaf area was higher in ammonium- than in nitrate-fed plants. Nitrate-fed plants had greater total leaf area in the presence of high carbon dioxide than in normal CO₂, due to an increase in epidermal cell size that led to development of larger leaflets with lower stomatal frequency. The observed changes in the morphology of roots and shoots agreed with the results observed for total biomass production. Nitrate-fed plants increased their biomass production by 100% in the presence of elevated CO₂ compared to 15% in ammonium-fed plants, indicating that the response of carob to high CO₂ concentrations is very dependent on the nitrogen source. Under elevated CO₂, nitrate grown plants had a larger content of sucrose in both roots and shoots, while no significant difference was observed in the content of sucrose in ammonium-grown plants, whether in ambient or enriched carbon dioxide. Hence, the differences in soluble carbohydrate contents can, at least partly, account for differences in root and shoot morphology. (C) 1997 Annals of Botany Company.

KEYWORDS: AMMONIUM ASSIMILATION, CELLULAR MECHANISMS, CERATONIA-SILYQUA, CO₂- ENRICHMENT, ELEVATED CO₂, GROWTH, NITRATE, PHOTOSYNTHESIS, PLANTS, RESPONSES

468

Csintalan, Z., Z. Tuba, H.K. Lichtenthaler, and J. Grace. 1996. Reconstitution of photosynthesis upon rehydration in the desiccated leaves of the poikilochlorophyllous shrub *Xerophyta scabrida* at elevated CO₂. *Journal of Plant Physiology* 148(3-4):345-350.

We report the resynthesis of the photosynthetic apparatus and the restoration of its function in the monocotyledonous C-3 shrub *Xerophyta scabrida* (Pax) Th. Dur. et Schinz (Velloziaceae) following a period of 5 years in the air-dried state. Detached leaves were rehydrated at present (350 $\mu\text{mol mol}^{-1}$) and at elevated CO₂ (700 $\mu\text{mol mol}^{-1}$). Elevated CO₂ concentration had no effect on the rate of rehydration, nor on the de novo resynthesis pattern of the chlorophylls and carotenoids or the development of photochemical activity in the reviving desiccated leaves. The time required to fully reconstitute the photosynthetic apparatus and its function in the air-dried achlorophyllous leaves on rehydration did not differ at the two CO₂ concentrations. However, respiratory activity during rehydration was more intensive and of longer duration at high CO₂ and net CO₂ assimilation first became apparent 12 h later than in the leaves rehydrated at present CO₂. After reconstitution

of the photosynthetic apparatus, the net CO₂ assimilation rate was higher in the high CO₂ leaves, however it rapidly declined to a value lower than that in the present CO₂ plants due to acclimation. This acclimation to elevated CO₂ occurred only after complete reconstitution of the photosynthetic apparatus. The downward acclimation of photosynthesis was accompanied by a decrease in content of photosynthetic pigments (chlorophyll a + b and carotenoids x + c) and stomatal conductance. The initial slope of the A/c(i) curve for the high CO₂ leaves was much lower and net CO₂ assimilation rates were lower at all c(i)'s than in the present CO₂ plants. The rate of respiration also decreased and the C- balance of the high CO₂ leaves therefore remained similar to that of leaves in present CO₂.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CAPACITY, EXPOSURE, PLANTS, RESPIRATION

469

Cui, M., P.M. Miller, and P.S. Nobel. 1993. CO₂ exchange and growth of the crassulacean acid metabolism plant *Opuntia ficus-indica* under elevated CO₂ in open-top chambers. *Plant Physiology* 103(2):519-524.

CO₂ uptake, water vapor conductance, and biomass production of *Opuntia ficus-indica*, a Crassulacean acid metabolism species, were studied at CO₂ concentrations of 370, 520, and 720 $\mu\text{mol L}^{-1}$ in open-top chambers during a 23-week period. Nine weeks after planting, daily net CO₂ uptake for basal cladodes at 520 and 720 $\mu\text{mol L}^{-1}$ of CO₂ was 76 and 98% higher, respectively, than at 370 $\mu\text{mol L}^{-1}$. Eight weeks after daughter cladodes emerged, their daily net CO₂ uptake was 35 and 49% higher at 520 and 720 $\mu\text{mol L}^{-1}$ of CO₂, respectively, than at 370 $\mu\text{mol L}^{-1}$. Daily water-use efficiency was 88% higher under elevated CO₂ for basal cladodes and 57% higher for daughter cladodes. The daily net CO₂ uptake capacity for basal cladodes increased for 4 weeks after planting and then remained fairly constant, whereas for daughter cladodes, it increased with cladode age, became maximal at 8 to 14 weeks, and then declined. The percentage enhancement in daily net CO₂ uptake caused by elevated CO₂ was greatest initially for basal cladodes and at 8 to 14 weeks for daughter cladodes. The chlorophyll content per unit fresh weight of chlorenchyma for daughter cladodes at 8 weeks was 19 and 62% lower in 520 and 720 $\mu\text{mol L}^{-1}$ of CO₂, respectively, compared with 370 $\mu\text{mol L}^{-1}$. Despite the reduced chlorophyll content, plant biomass production during 23 weeks in 520 and 720 $\mu\text{mol L}^{-1}$ of CO₂ was 21 and 55% higher, respectively, than at 370 $\mu\text{mol L}^{-1}$. The root dry weight nearly tripled as the CO₂ concentration was doubled, causing the root/shoot ratio to increase with CO₂ concentration. During the 23-week period, elevated CO₂ significantly increased CO₂ uptake and biomass production of *O. ficus-indica*.

KEYWORDS: AGAVE-VILMORINIANA, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, PHOTOSYNTHESIS, PRODUCTIVITY, RESPIRATION, RESPONSES, TEMPERATURE, WATER-USE, YIELD

470

Cui, M., and P.S. Nobel. 1994. Gas-exchange and growth-responses to elevated CO₂ and light levels in the CAM species *Opuntia ficus-indica*. *Plant, Cell and Environment* 17(8):935-944.

Gas exchange and dry-weight production in *Opuntia ficus-indica*, a CAM species cultivated worldwide for its fruit and cladodes, were studied in 370 and 750 $\mu\text{mol mol}^{-1}$ CO₂ at three photosynthetic photon flux densities (PPFD: 5, 13 and 20 $\text{mol m}^{-2} \text{d}^{-1}$). Elevated CO₂ and PPFD enhanced the growth of basal cladodes and roots during the 12-week study. A rise in the PPFD increased the growth of daughter cladodes; elevated CO₂ enhanced the growth of first-daughter cladodes but decreased the growth of the second-daughter cladodes produced on them. CO₂ enrichment enhanced daily net CO₂ uptake during the initial 8 weeks after planting for both basal and first- daughter cladodes. Water

vapour conductance was 9 to 15% lower in 750 than in 370 $\mu\text{mol}^{-1}\text{CO}_2$. Chlorophyll content was lower in elevated CO_2 and at higher PPFD. Soluble sugar and starch contents increased with time and were higher in elevated CO_2 and at higher PPFD. The total plant nitrogen content was lower in elevated CO_2 . The effect of elevated CO_2 on net CO_2 uptake disappeared at 12 weeks after planting, possibly due to acclimation or feedback inhibition, which in turn could reflect decreases in the sink strength of roots. Despite this decreased effect on net CO_2 uptake, the total plant dry weight at 12 weeks averaged 32% higher in 750 than in 370 $\mu\text{mol}^{-1}\text{CO}_2$. Averaged for the two CO_2 treatments, the total plant dry weight increased by 66% from low to medium PPFD and by 37% from medium to high PPFD.

KEYWORDS: AGAVE-VILMORINIANA, CARBON DIOXIDE, CO_2 -ENRICHMENT, CRASSULACEAN ACID METABOLISM, PHOTOSYNTHESIS, PHYSIOLOGY, PLANT GROWTH, PRODUCTIVITY, SHORT-TERM, WATER-USE EFFICIENCY

471

Cure, J.D., T.W. Rufty, and D.W. Israel. 1989. Alterations in soybean leaf development and photosynthesis in a CO_2 -enriched atmosphere. *Botanical Gazette* 150(4):337-345.

472

Cure, J.D., T.W. Rufty, and D.W. Israel. 1991. Assimilate relations in source and sink leaves during acclimation to a CO_2 -enriched atmosphere. *Physiologia Plantarum* 83(4):687-695.

Evidence from previous studies suggested that adjustments in assimilate formation and partitioning in leaves might occur over time when plants are exposed to enriched atmospheric CO_2 . We examined assimilate relations of source (primary unifoliolate) and developing sink (second mainstem trifoliolate) leaves of soybean [*Glycine max* (L.) Merr. cv. Lee] plants for 12 days after transfer from a control (350- $\mu\text{mol}^{-1}\text{CO}_2$) to a high (700- $\mu\text{mol}^{-1}\text{CO}_2$) environment. Similar responses were evident in the two leaf types. Net CO_2 exchange rate (CER) immediately increased and remained elevated in high CO_2 . Initially, the additional assimilate at high CO_2 levels in the light and was utilized in the subsequent dark period. After approximately 7 days, assimilate export in the light began to increase and by 12 days reached rates 3 to 5 times that of the control. In the developing sink leaf, high rates of export in the light occurred as the leaf approached full expansion. The results indicate that a specific acclimation process occurs in source leaves which increases the capacity for assimilate export in the light phase of the diurnal cycle as plants adjust to enriched CO_2 and a more rapid growth rate.

KEYWORDS: CO_2 -ENRICHMENT, ELEVATED CARBON-DIOXIDE, GROWTH, NITROGEN, PHOTOSYNTHESIS, PLANTS, SEED YIELD, STARCH FORMATION, TRANSLOCATION, WATER-STRESS

473

Curtis, P.S. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant, Cell and Environment* 19(2):127-137.

The response of trees to rising atmospheric CO_2 concentration ($[\text{CO}_2]$) is of concern to forest ecologists and global carbon modellers and is the focus of an increasing body of research work. I review studies published up to May 1994, and several unpublished works, which reported at least one of the following: net CO_2 assimilation (A), stomatal conductance (g(s)), leaf dark respiration (R(d)), leaf nitrogen or specific leaf area (SLA) in woody plants grown at <400 $\mu\text{mol}^{-1}\text{CO}_2$ or at 600-800 $\mu\text{mol}^{-1}\text{CO}_2$. The resulting data from 41 species were

categorized according to growth conditions (unstressed versus stressed), length of CO_2 exposure, pot size and exposure facility [growth chamber (GC), greenhouse (GH), or open-top chamber (OTC)] and interpreted using meta-analytic methods. Overall, A showed a large and significant increase at elevated $[\text{CO}_2]$ but length of CO_2 exposure and the exposure facility were important modifiers of this response. Plants exposed for <50 d had a significantly greater response, and those from GCs had a significantly lower response than plants from longer exposures or from OTC studies. Negative acclimation of A was significant and general among stressed plants, but in unstressed plants was influenced by length of CO_2 exposure, the exposure facility and/or pot size. Growth at elevated $[\text{CO}_2]$ resulted in moderate reductions in g(s) in unstressed plants, but there was no significant effect of CO_2 on g(s) in stressed plants. Leaf dark respiration (mass or area basis) was reduced strongly by growth at high $[\text{CO}_2]$, while leaf N was reduced only when expressed on a mass basis. This review is the first meta-analysis of elevated CO_2 studies and provides statistical confirmation of several general responses of trees to elevated $[\text{CO}_2]$. It also highlights important areas of continued uncertainty in our understanding of these responses.

KEYWORDS: ATMOSPHERIC CO_2 , CLUTCH-SIZE, CO_2 CONCENTRATION, DARK RESPIRATION, LIRIODENDRON-TULIPIFERA L, PHOSPHORUS DEFICIENCY, PINUS-RADIATA, SEEDLINGS, STOMATAL CONDUCTANCE, WATER-USE

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Curtis, P.S., L.M. Balduman, B.G. Drake, and D.F. Whigham. 1990. Elevated atmospheric CO_2 effects on belowground processes in C3 and C4 estuarine marsh communities. *Ecology* 71(5):2001-2006.

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Curtis, P.S., A.A. Snow, and A.S. Miller. 1994. Genotype-specific effects of elevated CO_2 on fecundity in wild radish (*Raphanus raphanistrum*). *Oecologia* 97(1):100-105.

Rising atmospheric CO_2 may lead to natural selection for genotypes that exhibit greater fitness under these conditions. The potential for such evolutionary change will depend on the extent of within-population genetic variation in CO_2 responses of wild species. We tested for heritable variation in CO_2 -dependent life history responses in a weedy, cosmopolitan annual, *Raphanus raphanistrum*. Progeny from five paternal families were grown at ambient and twice ambient CO_2 using outdoor open-top chambers (160 plants per CO_2 treatment). Elevated CO_2 stimulated net assimilation rates, especially in plants that had begun flowering. Across paternal families, elevated CO_2 led to significant increases in flower and seed production (by 22% and 13% respectively), but no effect was seen on time to bolting, leaf area at bolting, fruit set, or number of seeds per fruit. Paternal families differed in their response to the CO_2 treatment: in three families there were no significant CO_2 effects, while in one family lifetime fecundity increased by > 50%. These genotype-specific effects altered fitness rankings among the five paternal families. Although we did not detect a significant genotype X CO_2 interaction, our results provide evidence for heritable responses to elevated CO_2 . In a subset of plants, we found that the magnitude of CO_2 effects on fecundity was also influenced by soil fertility.

KEYWORDS: ATMOSPHERIC CO_2 , CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, INTRASPECIFIC VARIATION, L BRASSICACEAE, LIFE-HISTORY, SATIVUS L, SEED-WEIGHT VARIATION, SIZE VARIATION

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Curtis, P.S., and J.A. Teeri. 1992. Seasonal responses of leaf gas-

exchange to elevated carbon- dioxide in populus-grandidentata. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 22(9):1320-1325.

Rising atmospheric carbon dioxide concentrations may have important consequences for forest ecosystems. We studied above- and below-ground growth and leaf gas exchange responses of Populus grandidentata Michx. to elevated CO₂ under natural forest conditions over the course of a growing season. Recently emerged P. grandidentata seedlings were grown in native, nutrient-poor soils at ambient and twice ambient (707 mubar (1 bar = 100 kPa)) CO₂ partial pressure for 70 days in open-top chambers in northern lower Michigan. Total leaf area and shoot and root dry weight all increased in high CO₂ grown plants. Photosynthetic light and CO₂ response characteristics were measured 28, 45, and 68 days after exposure to elevated CO₂. In ambient grown plants, light saturated assimilation rates increased from day 28 to day 45 and then declined at day 68 (15 September). This late-season decline, typical of senescing Populus leaves, was due both to a decrease in the initial slope of the net CO₂ assimilation versus intercellular CO₂ Partial pressure relationship and to decreased CO₂ saturated assimilation rates. Specific leaf nitrogen (mg N . (cm² leaf area)⁻¹) did not change during this period, although leaf carbon content and leaf weight (mg . cm⁻²) both increased. In ambient grown plants stomatal conductance also declined at day 68. In contrast, plants grown at elevated CO₂ showed no late- season decline in photosynthetic capacity or changes in leaf weight, suggesting a delay in senescence with long-term exposure to high CO₂. High CO₂ grown plants also maintained photosynthetic sensitivity to increasing C(i) throughout the exposure period, while ambient CO₂ grown plants were insensitive to C(i) above 400 mubar on day 68. These results indicate the potential for direct CO₂ fertilization of P. grandidentata in the field and provide evidence for a new mechanism by which elevated atmospheric CO₂ could influence seasonal carbon gain.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂ ENRICHMENT, GROWTH-RESPONSES, IRRADIANCE, LEAVES, LIQUIDAMBAR-STYRACIFLUA, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, PINUS-TAEDA SEEDLINGS, VEGETATION

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Curtis, P.S., C.S. Vogel, K.S. Pregitzer, D.R. Zak, and J.A. Teeri. 1995. Interacting effects of soil fertility and atmospheric co₂ on leaf-area growth and carbon gain physiology in populus X euramericana (dode) guinier. *New Phytologist* 129(2):253-263.

Two important processes which may limit productivity gains in forest ecosystems with rising atmospheric CO₂ are reduction in photosynthetic capacity following prolonged exposure to high CO₂ and diminution of positive growth responses when soil nutrients, particularly N, are limiting. To examine the interacting effects of soil fertility and CO₂ enrichment on photosynthesis and growth in trees we grew hybrid poplar (Populus x euramericana) for 158 d in the field at ambient and twice ambient CO₂ and in soil with low or high N availability. We measured the timing and rate of canopy development, the seasonal dynamics of leaf level photosynthetic capacity, respiration, and N and carbohydrate concentration, and final above- and belowground dry weight. Single leaf net CO₂ assimilation (A) increased at elevated CO₂ over the majority of the growing season in both fertility treatments. At high fertility, the maximum size of individual leaves, total leaf number, and seasonal leaf area duration (LAD) also increased at elevated CO₂, leading to a 49% increase in total dry weight. In contrast, at low fertility leaf area growth was unaffected by CO₂ treatment. Total dry weight nonetheless increased 25% due to CO₂ effects on A. Photosynthetic capacity (A at constant internal p(CO₂), (C-i)) was reduced in high CO₂ plants after 100 d growth at low fertility and 135 d growth at high fertility. Analysis of A responses to changing C-i indicated that this negative adjustment of photosynthesis was due to a reduction in the maximum rate of CO₂ fixation by Rubisco. Maximum rate of electron transport and phosphate

regeneration capacity were either unaffected or declined at elevated CO₂. Carbon dioxide effects on leaf respiration were most pronounced at high fertility, with increased respiration mid-season and no change (area basis) or reduced (mass basis) respiration late- season in elevated compared to ambient CO₂ plants. This temporal variation correlated with changes in leaf N concentration and leaf mass per area. Our results demonstrate the importance of considering both structural and physiological pathways of net C gain in predicting tree responses to rising CO₂ under conditions of suboptimal soil fertility.

KEYWORDS: DIOXIDE CONCENTRATION, DRY-MATTER, ELEVATED CO₂, ENRICHMENT, FEEDBACK, GAS-EXCHANGE, NITROGEN, PHOTOSYNTHESIS, PLANTS, SHORT- TERM

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Curtis, P.S., and X.Z. Wang. 1998. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113(3):299-313.

Quantitative integration of the literature on the effect of elevated CO₂ on woody plants is important to aid our understanding of forest health in coming decades and to better predict terrestrial feedbacks on the global carbon cycle. We used meta-analytic methods to summarize and interpret more than 500 reports of effects of elevated CO₂ on woody plant biomass accumulation and partitioning, gas exchange, and leaf nitrogen and starch content. The CO₂ effect size metric we used was the log-transformed ratio of elevated compared to ambient response means weighted by the inverse of the variance of the log ratio. Variation in effect size among studies was partitioned according to the presence of interacting stress factors, length of CO₂ exposure, functional group status, pot size, and type of CO₂ exposure facility. Both total biomass (WT) and net CO₂ assimilation (A) increased significantly at about twice ambient CO₂, regardless of growth conditions. Low soil nutrient availability reduced the CO₂ stimulation of WT by half, from + 31 % under optimal conditions to + 16 %, while low light increased the response to + 52 %. We found no significant shifts in biomass allocation under high CO₂. Interacting stress factors had no effect on the magnitude of responses of A to CO₂, although plants grown in growth chambers had significantly lower responses (+ 19 %) than those grown in greenhouses or in open-top chambers (+ 54 %). We found no consistent evidence for photosynthetic acclimation to CO₂ enrichment except in trees grown in pots < 0.51 (- 36 %) and no significant CO₂ effect on stomatal conductance. Both leaf dark respiration and leaf nitrogen were significantly reduced under elevated CO₂ (- 18 % and - 16 % respectively, data expressed on a leaf mass basis), while leaf starch content increased significantly except in low nutrient grown gymnosperms. Our results provide robust, statistically defensible estimates of elevated CO₂ effect sizes against which new results may be compared or for use in forest and climate model parameterization.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BETULA-PENDULA ROTH, CASTANEA-SATIVA MILL, LEAF GAS-EXCHANGE, LOBLOLLY-PINE SEEDLINGS, NET PRIMARY PRODUCTION, PICEA-ABIES L, QUERCUS-ALBA, RELATIVE GROWTH-RATE, STOMATAL CONDUCTANCE

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Curtis, P.S., D.R. Zak, K.S. Pregitzer, and J.A. Teeri. 1994. Aboveground and belowground response of populus grandidentata to elevated atmospheric co₂ and soil n-availability. *Plant and Soil* 165(1):45-51.

Soil N availability may play an important role in regulating the long-term responses of plants to rising atmospheric CO₂ partial pressure. To further examine the linkage between above- and belowground C and N cycles at elevated CO₂, we grew clonally propagated cuttings of Populus

grandidentata in the field at ambient and twice ambient CO₂ in open bottom root boxes filled with organic matter poor native soil. Nitrogen was added to all root boxes at a rate equivalent to net N mineralization in local dry oak forests. Nitrogen added during August was enriched with N-25 to trace the flux of N within the plant-soil system. Above- and belowground growth, CO₂ assimilation, and leaf N content were measured non-destructively over 142 d. After final destructive harvest, roots, stems, and leaves were analyzed for total N and N-15. There was no CO₂ treatment effect on leaf area, root length, or net assimilation prior to the completion of N addition. Following the N addition, leaf N content increased in both CO₂ treatments, but net assimilation showed a sustained increase only in elevated CO₂ grown plants. Root relative extension rate was greater at elevated CO₂, both before and after the N addition. Although final root biomass was greater at elevated CO₂, there was no CO₂ effect on plant N uptake or allocation. While low soil N availability severely inhibited CO₂ responses, high CO₂ grown plants were more responsive to N. This differential behavior must be considered in light of the temporal and spatial heterogeneity of soil resources, particularly N which often limits plant growth in temperate forests.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, QUERCUS-ALBA, SEEDLING GROWTH, TREES

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Cushman, J.C., and H.J. Bohnert. 1997. Molecular genetics of Crassulacean acid metabolism. *Plant Physiology* 113(3):667-676.

Most higher plants assimilate atmospheric CO₂ through the C-3 pathway of photosynthesis using ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). However, when CO₂ availability is reduced by environmental stress conditions, the incomplete discrimination of CO₂ over O₂ by Rubisco leads to increased photorespiration, a process that reduces the efficiency of C-3 photosynthesis. To overcome the wasteful process of photorespiration, approximately 10% of higher plant species have evolved two alternate strategies for photosynthetic CO₂ assimilation, C-3 photosynthesis and Crassulacean acid metabolism. Both of these biochemical pathways employ a "CO₂ pump" to elevate intracellular CO₂ concentrations in the vicinity of Rubisco, suppressing photorespiration and therefore improving the competitiveness of these plants under conditions of high light intensity, high temperature, or low water availability. This CO₂ pump consists of a primary carboxylating enzyme, phosphoenolpyruvate carboxylase. In C-4 plants, this CO₂-concentrating mechanism is achieved by the coordination of two carboxylating reactions that are spatially separated into mesophyll and bundle-sheath cell types (for review, see R.T. Furbank, W.C. Taylor [1995] *Plant Cell* 7:797-802; M.S.B. Ku, Y. Kano-Murakami, M. Matsuoka [1996] *Plant Physiol* 111:949-957). In contrast, Crassulacean acid metabolism plants perform both carboxylation reactions within one cell type, but the two reactions are separated in time. Both pathways involve cell-specific changes in the expression of many genes that are not present in C-3 plants.

KEYWORDS: ABSCISIC- ACID, C-3 PHOTOSYNTHESIS, CAM, COMMONICE PLANT, DIFFERENTIAL EXPRESSION, INDUCTION, MESEMBRYANTHEMUM-CRYSTALLINUM L, NADP-MALIC ENZYME, PHOSPHOENOLPYRUVATE CARBOXYLASE, SALT STRESS

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Dacey, J.W.H., B.G. Drake, and M.J. Klug. 1994. Stimulation of methane emission by carbon-dioxide enrichment of marsh vegetation. *Nature* 370(6484):47-49.

THERE is substantial evidence that many plants respond to increased concentrations of atmospheric carbon dioxide by increasing their

productivity(1-4) This observation has led to the suggestion that, by taking up CO₂, the terrestrial biosphere might mitigate the potential greenhouse warming associated with anthropogenic CO₂ emissions(5). Whiting and Chanton(6) have found, however, that for wetlands of varying productivity around the world, higher net primary production is associated with higher emissions of methane-another important greenhouse gas. Here we present measurements of methane emissions from a marsh that has been exposed to twice the present ambient concentration of atmospheric CO₂. We find that over a one-week period, the CO₂-enriched sites had significantly higher emissions of methane than the control sites. Our results suggest that future increases in atmospheric CO₂ concentration may lead to significant increases in methane emissions from wetlands.

KEYWORDS: COMMUNITIES, ELEVATED CO₂, ESTUARINE MARSH, FIELD, GROWTH, PLANTS, PRODUCTIVITY, RESPONSES, RICE PADDIES, WETLANDS

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Dahlman, R.C. 1993. Co₂ and plants - revisited. *Vegetatio* 104:339-355.

The decade-long USA research program on the direct effects of CO₂ enrichment on vegetation has achieved important milestones and has produced a number of interesting and exciting findings. Research beginning in 1980 focused on field experiments to determine whether phenomena observed in the laboratory indeed occurred in natural environments. The answer is yes. Data obtained from numerous field studies show mixed response of crop and native species to CO₂ enrichment however. Nearly all experiments demonstrate that plants exhibit positive gain when grown at elevated CO₂; although the magnitude varies greatly. Most crop responses range from 30 to 50 % increase in yield. Results from long-term experiments with woody species and ecosystems are even more variable. Huge growth responses (100 to nearly 300 % increase relative to controls) are reported from several tree experiments and the salt-marsh ecosystem experiment. Other results from experiments with woody species and the tundra ecosystem suggest little no effect of CO₂ on physiology, growth or productivity. Numerous studies of the physiology of the CO₂ effect are continuing in attempts to understand controlling mechanisms and to explain the variable growth responses. Particular emphasis needs to be given to physiological measures of interactions involving the CO₂ effect and other environmental influences, and to the wide-ranging observations of photosynthesis acclimation to CO₂. Prospects for future research are identified.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED LEVELS, ENRICHMENT, GROWTH, INHIBITION, PHOTOSYNTHESIS, SEEDLINGS, SHORT- TERM, TEMPERATURE

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Dale, H., and M.C. Press. 1998. Elevated atmospheric CO₂ influences the interaction between the parasitic angiosperm *Orobanche minor* and its host *Trifolium repens*. *New Phytologist* 140(1):65-73.

The influence of the root holoparasitic angiosperm *Orobanche minor* Sm. on the biomass, photosynthesis, carbohydrate and nitrogen content of *Trifolium repens* L. was determined for plants grown at two CO₂ concentrations (350 and 550 $\mu\text{mol mol}^{-1}$). Infected plants accumulated less biomass than their uninfected counterparts, although early in the association there was a transient stimulation of growth. Infection also influenced biomass allocation both between tissues (infected plants had lower root:shoot ratios) and within tissues: infected roots were considerably thicker before the point of parasite attachment and thinner below. Higher concentrations of starch were also found in roots above the point of attachment, particularly for plants grown in