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Growth and Root NO_3^- and PO_4^{3-} Uptake Capacity of Three Desert Species in Response to Atmospheric CO_2 Enrichment

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Abstract. In a phytotron experiment, we examined growth and rates of NO_3^- and PO_4^{3-} 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 CO_2 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 NO_3^- and PO_4^{3-} . Elevated CO_2 increased total biomass by 69 and 55% in *Larrea* and *Prosopis* seedlings and by 25% in *Bouteloua*. NO_3^- and PO_4^{3-} uptake rates were more than doubled in *Bouteloua* at high compared to ambient CO_2 . In contrast, CO_2 enrichment inhibited root NO_3^- uptake capacity in *Larrea* by about 55% without a significant effect on PO_4^{3-} absorption rate; rates of NO_3^- and PO_4^{3-} and uptake in *Prosopis* were insensitive to CO_2 treatment. Elevated CO_2 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 CO_2 , 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 CO_2 .

Keywords: *Bouteloua eriopoda*, *Larrea tridentata*, *Prosopis glandulosa*, elevated CO_2 , root nutrient absorption capacity

Introduction

Short-term exposure to CO_2 enrichment often stimulates growth and photosynthetic C fixation. In most natural ecosystems, however, long-term growth and photosynthetic responses may be confined by the limited availability of mineral nutrients, particularly N and P (Bazzaz 1990; Conroy 1992; Sinclair 1992; McKee and Woodward 1994). Therefore, factors that may affect availability and uptake of nutrients are critical in determining plant and ecosystem responses to high CO_2 .

Numerous factors, e.g. microbial activities, soil solution concentration, mass flow and diffusion may limit nutrient availability at the root surface, but compensatory adjustments in root size and/or active uptake capacity may ameliorate such limitations (Nye and Tinker 1977; Chapin 1980; Barber 1984). Yet it is presently unknown if root growth and physiological properties can positively adjust to meet increased plant N and P demand under high CO_2 . According to whole-plant models of C and nutrient balance, resources of abundant availability should be allocated for the acquisition of the most limiting resources (Chapin 1980; Clarkson 1985; Johnson 1985; Robinson 1986; Ågren and Ingstad 1987). Considering that elevated CO_2 often

improves the whole plant and root carbon status (Norby *et al.* 1987; Tschaplinski *et al.* 1993; BassiriRad *et al.* 1996), one may expect a greater allocation of C for root growth and/or active nutrient uptake in response to CO_2 enrichment.

Although studies addressing compensatory root growth often indicate a favorable root vs shoot growth in response to high CO_2 , these shifts are often subtle and obscured by experimental artifacts (Stulen and den Hertog 1993; Norby 1994; Rogers *et al.* 1994). Furthermore, a mere increase in root biomass allocation is a poor index of nutrient acquisition, particularly in woody roots where a large proportion of biomass is invested in tap roots or other highly suberised roots that are not involved in active nutrient uptake. There is even less information available about the direct effects of CO_2 on active root nutrient absorption (BassiriRad *et al.* 1996). A common short-term response of C_3 species to CO_2 enrichment includes enhanced growth accompanied by a reduction in foliar nutrient concentration, particularly that of N (Hocking and Meyer 1991; Conroy 1992; Baxter *et al.* 1994; Rogers *et al.* 1996). These observations have been interpreted to indicate that high CO_2 reduces the rate of root nutrient uptake relative to C gain (O'Neill *et al.* 1987; Conroy 1992; Bowes 1993). However,

an accelerated decline in tissue nutrient concentration, in addition to uptake and transport capacity of the root, can be influenced by a suite of other processes such as changes in nutrient use efficiency and remobilisation, dilution due to growth and accumulation of starch, changes in root to shoot ratio, and developmental stages of growth. A mechanistic understanding of how elevated CO₂ may affect plant nutrient status and long-term growth responses must include direct measurements of root nutrient absorption capacity.

Elevated CO₂ may also affect root nutrient uptake capacity among species to a different extent, thus altering competitive interactions which have significant implications for ecosystem response to CO₂. In this study we examined changes in the rates of root NO₃⁻ and PO₄³⁻ uptake (per gram dry mass of fine roots) and growth responses of two C₃ perennial woody shrubs, *Larrea tridentata* and *Prosopis glandulosa*, and a C₄ perennial grass, *Bouteloua eriopoda* to the doubling of the atmospheric CO₂ concentration. Specifically, we aimed to address:

Does elevated CO₂ elicit compensatory changes in root N and P uptake capacity?

Are these compensatory responses differentially expressed among species?

Do these interspecies differences in root responses determine the direction and the magnitude of changes in tissue nutrient status under high CO₂?

Although these are dominant species of many hot deserts of south-western USA and play a major role in how arid ecosystems may respond to climate change (Schlesinger *et al.* 1990; Reynolds *et al.* 1996), their potential responses to high CO₂ have yet to be examined.

Materials and Methods

Plant Materials and Growth Conditions

This experiment was conducted at the Duke University Phytotron. Seeds of all three species were collected from NSF LTER field site at the Jornada Experimental Range near Las Cruces, New Mexico. After germination, uniformly sized seedlings were transferred into 4 L pots containing fine sand, i.e. one seedling per pot for *Larrea* and *Prosopis* and five seedlings per pot for *Bouteloua*. There were 5–10 replicate pots per treatment. These species differ in their growth rates; therefore, to conduct the uptake experiment on relatively comparably sized seedlings, we staggered the planting dates as follows; *Larrea* on 18 March 1993, *Prosopis* on 22 May 1993 and *Bouteloua* on 29 May 1993. Seedlings were subsequently grown in an environmentally regulated walk-in growth chamber that was maintained at a day/night air temperature of 30/20°C, PAR of 1000 μmol m⁻² s⁻¹ with a 16 h photoperiod, atmospheric partial pressure of 35 Pa and an average relative humidity of 70%. Each pot was irrigated to free drainage on alternate days with either water or a 1/4 strength modified Hoagland solution. The solution pH was adjusted to 7 and concentrations (ppm) of the macronutrients were: NO₃⁻-N (23), K (60), P (16), Ca (51), S (33), and Mg (12). On 27 April 1993 we began the CO₂ treatment by transferring the seedlings into two

similar size chambers that were set at a CO₂ partial pressure of 35 or 70 Pa. All other environmental conditions were maintained as described earlier.

Uptake Studies

Two and a half months after the CO₂ treatments began, rates of NO₃⁻ and PO₄³⁻ uptake of intact root systems were determined using depletion of these ions from well-aerated hydroponic solutions. Individual seedlings were removed from pots and the adhering soil was gently rinsed from the roots before they were transplanted into 2 L tightly sealed plastic containers filled with the nutrient solution (as above). Because the fine sand did not strongly adhere to the root surfaces, we had very little loss of fine roots during the transplant procedure. After the transplant, seedlings were grown in this solution for an additional week under their previous growth conditions to overcome transplanting shock. During this equilibration period, the nutrient solution was renewed every other day.

On the day of the actual uptake study, all seedlings were supplied with a new solution about 2 h into the photoperiod and the changes in NO₃⁻ and PO₄³⁻ were analysed on 10 mL solution samples taken at the beginning and at the end of a 4 h uptake period. Composition of the uptake solution was identical to that used above but at only half the concentration. Concentrations of the ions in the sample solution were measured using a TRACCS 800 Continuous Flow Analytical System (Bran+Luebbe Analyzing Technologies, Inc., Technical Industrial Systems Corp., Elmsford, NY). Water loss by transpiration was measured by weighing individual containers during the uptake period and the amount lost was replaced with distilled water before the final sample was taken. Net uptake rate was calculated from changes in solution concentration of each ion per g dry wt of roots per hour. Only the dry mass of the fine roots (see below) was used in calculating the uptake rate. Uptake measurements and growth during the equilibration period were conducted under the corresponding treatment conditions.

Biomass, N and P Analysis

Following the uptake study, all seedlings were separated into root and shoot for dry mass determination. In shrubs, roots were further subdivided between fine active roots (white and light brown roots < 2 mm in diameter) and coarse roots (dark-colored roots > 2 mm in diameter). Because coarse roots were highly suberised and likely to be inactive for nutrient uptake, only fine root biomass was used to calculate nutrient uptake rate in *Larrea* and *Prosopis*. In contrast, roots of *Bouteloua* were uniform in size (< 2 mm in diameter) and appearance (predominantly white) and, at least in our study, were not differentiated into fine and coarse roots. Hence, in *Bouteloua*, the whole root system was considered active in nutrient uptake. All plant parts were dried to a constant mass at 60°C. Total N and P concentrations were measured on dried foliar and fine root tissues. Subsamples (approximately 20 mg) were digested using a sulfuric acid–hydrogen peroxide flux (Lowther 1980) and the digests were analysed for total N and P as described earlier. *Prosopis* is a legume and is capable of a significant N uptake through N₂ fixation in the field, but seedlings used here were uninfected and non-nodulated. Therefore, tissue N concentration reported here is exclusively a function of root N uptake.

Statistics

Differences between the CO₂ treatments were analysed using one-way ANOVA. Data were tested for normal distribution and were log- or square-root transformed when necessary. The Scheffe-box test (Sokal and Rohlf 1981) was used for mean separation of the dependent variables for each species and to test the homogeneity of the variances.

Results

Growth

Seventy five days after the initiation of CO₂ treatments, whole plant dry mass was significantly enhanced in response to CO₂ enrichment in all three species (Fig. 1). Increased total biomass was, however, more pronounced in *Larrea* and *Prosopis* than in *Bouteloua*, i.e. increased biomass in response to elevated CO₂ was 25% in *Bouteloua*, but 69 and

55% in *Larrea* and *Prosopis*, respectively. Both below- and above-ground components were significantly enhanced in *Bouteloua*, but the below-ground biomass (fine and coarse roots) was not significantly affected by the CO₂ treatments in the C₃ shrubs (Fig. 1). Consequently, the fraction of total biomass allocated to shrub fine roots significantly ($P \leq 0.001$) decreased in response to elevated CO₂, but this fraction was significantly ($P \leq 0.01$) increased in *Bouteloua*. The pattern of the above-ground biomass allocation at high CO₂ varied considerably between the two shrubs, with *Larrea* showing significant increases in both autotrophic (leaf) and heterotrophic (stem) tissues whereas increased above-ground biomass in *Prosopis* was principally invested in the stem tissues (Fig. 1).

Nutrient Uptake

Rates of root NO₃⁻ and PO₄³⁻ uptake were markedly different among species at ambient CO₂, with *Prosopis* showing the lowest uptake capacity for either nutrients (Fig. 2). Elevated CO₂ differentially affected root nutrient uptake capacity among all species. Nitrate and phosphate uptake rates were more than doubled in *Bouteloua* at high compared to ambient CO₂ (Fig. 2). In contrast, CO₂ enrichment

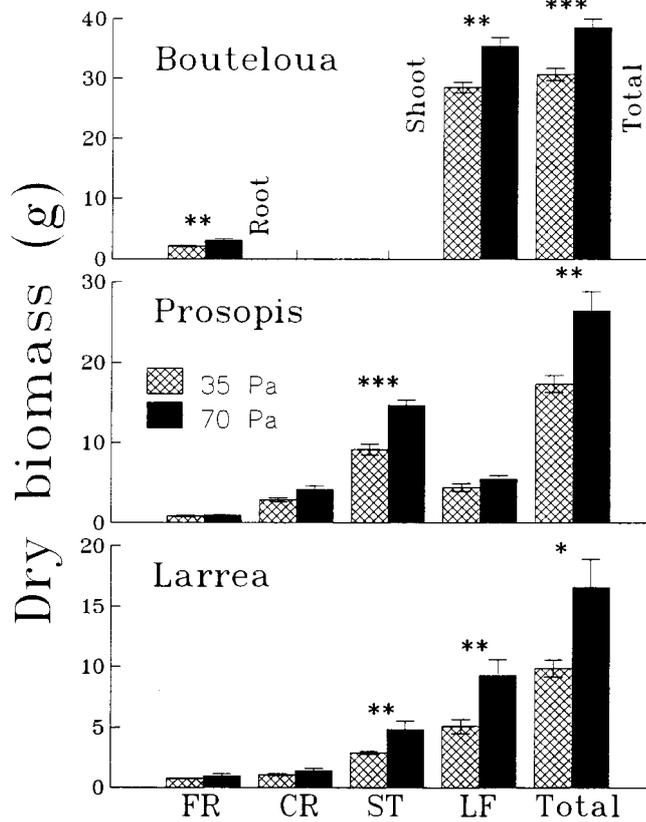


Fig. 1. Total biomass production and partitioning in three desert species in response to ambient and double the ambient CO₂ concentration. Abbreviations FR, CR, ST and LF refer to fine roots, coarse roots, stem and leaf. Roots < 2 mm in diameter were designated as fine and those > 2 mm were designated as coarse. Under high CO₂, the fraction of total biomass allocated to fine roots increased by 20% in *Bouteloua* ($P < 0.05$), but decreased by 30 and 25% ($P < 0.01$) in *Larrea* and *Prosopis*, respectively. Values are means \pm 1 s.e. ($n = 6$) and the statistical differences are denoted by: *, $P < 0.05$, **, $P < 0.01$ and ***, $P < 0.001$.

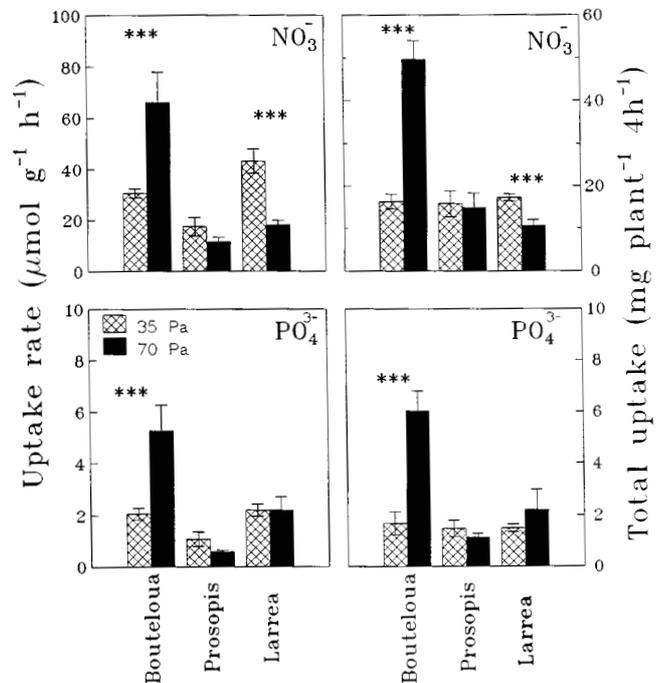


Fig. 2. Rates of NO₃⁻ and PO₄³⁻ uptake by roots of *Bouteloua*, *Prosopis* and *Larrea* grown at ambient or double the ambient CO₂ concentration. Values are means \pm 1 s.e. ($n = 6$) and the statistical differences are denoted by: *, $P < 0.05$, **, $P < 0.01$ and ***, $P < 0.001$.

inhibited root NO_3^- uptake capacity by about 55% and had little effect on root PO_4^{3-} uptake rate in *Larrea*. Uptake rates of both NO_3^- and PO_4^{3-} did not significantly respond to changes in growth CO_2 concentrations in *Prosopis*. The direction and magnitude of uptake responses, expressed on a per-plant basis, were similar to those observed in uptake rates expressed on a root dry weight basis (Fig. 2).

Tissue N and P Concentrations

Doubling of the atmospheric CO_2 did not significantly alter leaf or fine root N concentration in *Bouteloua* (Table 1). In contrast, leaf N concentration was significantly lower in *Larrea* and *Prosopis* seedlings grown at high CO_2 . Elevated CO_2 also led to a significant decrease in leaf P concentration in *Larrea*, but foliar P concentration in *Prosopis* was not significantly affected in response to CO_2 (Table 1). Fine root concentration of N was not significantly different between the CO_2 treatments in all three species. However, fine root concentration of P was differentially affected in response to CO_2 enrichment, i.e. *Bouteloua* and *Prosopis* exhibited a significantly lower P concentration in the fine roots, but that concentration in *Larrea* was not significantly altered in response to high CO_2 .

Discussion

Elevated CO_2 had a more pronounced effect on productivity of the C_3 species, *Larrea* and *Prosopis*, than *Bouteloua*. The greater biomass responses of the shrub species relative to the grass at high CO_2 may be due to differences in C_3 vs C_4 pathways. That the elevated CO_2 should have a greater impact on biomass accumulation of C_3 than C_4 species is consistent with predicted theoretical responses of these two photosynthetic pathways (Björkman and Pearcy 1983) and with numerous empirical observations (Wong 1979; Bazzaz and Carlson 1984; Patterson *et al.* 1984; Wray and Strain 1987; Dippery *et al.* 1995). Changes

in biomass partitioning in response to CO_2 was species dependent. While elevated CO_2 led to significant increases in root and shoot fraction in *Bouteloua*, the C_3 shrubs allocated a larger proportion of total biomass to the aboveground tissues (Fig. 1). The proportion of biomass allocated to the fine roots, which is the fraction most important for nutrient absorption, increased by 17% in *Bouteloua*, but decreased by at least 30% in both *Larrea* and *Prosopis* at elevated CO_2 (Fig. 1).

In addition to its positive adjustment in root size, *Bouteloua* was also the only species that exhibited an enhanced root absorption capacity for both NO_3^- and PO_4^{3-} at high CO_2 (Fig. 2). Such species-dependent root responses may, at least in part, explain why tissue N and P concentration was maintained in the C_4 grass but not in its C_3 shrub counterparts (Table 1). The dichotomy of responses observed in nutrient relations of species studies here is consistent with the literature i.e. although elevated CO_2 commonly results in lower tissue N concentration, this effect is not universal (Vessey *et al.* 1990; Conroy 1992; Baxter *et al.* 1994; Rogers *et al.* 1996).

Of course, some of this controversy can be attributed to non-uniform growth conditions between experiments, but other factors are also involved. For example, excessive starch accumulation in some species may lead to nutrient dilution (Kuehny *et al.* 1991; Thomas and Strain 1991). Coleman *et al.* (1993, 1994) recently reported no differences in tissue N concentration of *Abutilon* and *Amaranthus* at high vs ambient CO_2 if plants of similar size rather than similar age were compared. He therefore argued that reduced tissue N concentration in response to CO_2 enrichment is caused by a size-dependent ontogenic drift. Future research designed to evaluate mechanisms by which plant nutrient status and growth respond to CO_2 must address all of the above factors. We suggest that CO_2 enrichment can have a pronounced effect on root nutrient

Table 1. Total N and P concentrations in leaves and fine roots of three desert species as affected by growth CO_2 partial pressures

Values are means \pm 1 s.e. ($n = 6$) and within-species means followed by different letters are significantly different at $P < 0.05$

Species	Growth CO_2 (Pa)	Concentration (mg g^{-1})			
		Leaves		Fine Roots	
		N	P	N	P
<i>Bouteloua</i>	35	18.9 \pm 1.2	2.7 \pm 0.1a	16.9 \pm 0.7	3.1 \pm 0.2b
	70	22.4 \pm 0.7	3.3 \pm 0.1b	15.4 \pm 0.5	2.2 \pm 0.2a
<i>Prosopis</i>	35	41.1 \pm 1.1b	2.0 \pm 0.3	34.1 \pm 0.7	13.7 \pm 1.4b
	70	26.4 \pm 0.3a	2.1 \pm 0.1	33.9 \pm 0.7	6.5 \pm 1.0a
<i>Larrea</i>	35	23.8 \pm 1.9b	5.1 \pm 0.5b	31.1 \pm 0.6	4.4 \pm 0.2
	70	16.9 \pm 1.1a	3.5 \pm 0.3a	30.0 \pm 1.0	3.9 \pm 0.4

absorption capacity with significant implication for plant nutrient relations under high CO₂, and must therefore be an integral part of models designed to predict plant and ecosystem responses to high CO₂. Under field conditions, factors that influence fluxes of nutrients to the root surface are also critical in determining plant nutrient status in response to CO₂.

It is unclear why *Bouteloua* exhibited an elevated root uptake capacity for N and P in response to CO₂, whereas these rates were either unaffected in the C₃ species or inhibited, as was the case in root NO₃⁻ uptake rate in *Larrea*. Because uptake of both of these ions are energy-requiring processes, it may be useful to evaluate whether the supply of carbon substrate for respiration to the root is differentially affected in C₃ and C₄ species at high CO₂. In field-grown loblolly pine, we showed a strong correlation between enhanced root NO₃⁻ uptake kinetics and fine root carbohydrate status (BassiriRad *et al.* 1996). Uptake of both NO₃⁻ and PO₄³⁻ by roots of higher plants are also regulated by a negative feedback control (Lefebvre and Glass 1982; Siddiqi *et al.* 1990), i.e. increased root internal concentration of N and P can inhibit further uptake. Alternatively, root absorption capacity has been shown to be inversely related to nutrient status of the shoot (Chapin 1980).

In this study neither shoot demand, as defined by leaf N and P concentration, nor the root concentration of these ions could account for the observed responses in specific root uptake rates. For example, the higher root NO₃⁻ and PO₄³⁻ absorption rates exhibited in *Bouteloua* at high compared to ambient CO₂ were accompanied by no significant changes in leaf and root N and P concentration (Fig. 2 and Table 1). Furthermore, in *Larrea*, the decrease in leaf and fine root N concentration in response to CO₂ enrichment was associated with a marked inhibition of root NO₃⁻ uptake capacity (Fig. 2 and Table 1).

In summary, we found that, even though growth of *Bouteloua* in response to high CO₂ was not stimulated to the same extent as it was for the co-occurring shrubs, *Bouteloua* showed a greater capacity to acquire nutrient resources than its C₃ counterparts. The differential effects of CO₂ on nutrient procurement among these species corresponded largely to changes in their active nutrient uptake in response to high CO₂. These results must be interpreted with caution, but the primary indication is that compensatory adjustments in root size and activity may be critical in determining plant nutrient status in a changing global climate. We are currently exploring the mechanisms by which CO₂ may alter active root nutrient uptake. Interspecies differences in nutrient acquisition rate in response to increased atmospheric CO₂ may also have significant implications for competitive interactions among species and ecosystem-level patterns of C and N cycling, although such conclusions will remain hypothetical for now.

These species occupy sites that are not markedly different in nutrient availability but, during the last 100 years, overgrazing and recurring drought has lead to increasing replacement of *Bouteloua* by *Prosopis* and *Larrea*. Management plans targeting grazing practices have been somewhat successful in curbing and/or reversing shrub encroachment. However, changes in global and regional climate will remain an important factor determining species composition in these ecosystems. We speculate that long-term CO₂ exposure may favor *Bouteloua* as opposed to the C₃ shrubs due to its greater capacity for nutrient acquisition. Further studies are, however, needed to evaluate the relative performance of these species in response to CO₂ enrichment by including factors such as competition, water and N limitation.

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References

- Ågren, G. I., and Ingstad, T. (1987). Root : shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant, Cell and Environment* **10**, 579–586.
- Barber, S. A. (1984). 'Soil Nutrient Bioavailability. A Mechanistic Approach.' pp. 55–89. (John Wiley & Sons: New York.)
- BassiriRad, H., Thomas, R. B., Reynolds, J. F., and Strain, B. R. (1996). Differential responses of root uptake kinetics of NH₄⁺ and NO₃⁻ to enriched atmospheric CO₂ in field-grown loblolly pine. *Plant, Cell and Environment* **19**, 367–371.
- Baxter, R., Gantley, M., Ashenden, T. W., and Farrar, J. F. (1994). Effects of elevated carbon dioxide on three grass species from montane pasture. II. Nutrient uptake, allocation and efficiency of use. *Journal of Experimental Botany* **278**, 1267–1278.
- Bazzaz, F. A., and Carlson, R. W. (1984). The response of plants to elevated CO₂. I. Competition among an assemblage of annuals at two levels of soil moisture. *Oecologia* **62**, 196–198.
- Bazzaz, F. A. (1990). The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics* **21**, 167–196.
- Björkman, O., and Percy, R. W. (1983). Physiological effects. In 'CO₂ and Plants: the Response of Plants to Rising Levels of Atmospheric Carbon Dioxide'. (Ed E. R. Lemon.) pp. 65–106. (Westview Press: Boulder.)

- Bowes, G.** (1993). Facing the inevitable: plants and increasing atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology* **44**, 309–332.
- Chapin, F. S. III** (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**, 233–260.
- Clarkson, D. T.** (1985). Factors affecting mineral nutrient acquisition by plants. *Annual Review of Plant Physiology* **36**, 77–115.
- Coleman, J. S., McConnaughay, K. D. M., and Bazzaz, F. A.** (1993). Elevated CO₂ and plant nitrogen-use: is reduced tissue nitrogen concentration size-dependent? *Oecologia* **93**, 195–200.
- Coleman, J. S., McConnaughay, K. D. M., and Ackerly, D. D.** (1994). Interpreting phenotypic variation in plants. *TREE* **9**(5), 187–191.
- Conroy, J. P.** (1992). Influence of elevated atmospheric CO₂ concentrations on plant nutrition. *Australian Journal of Botany* **40**, 445–456.
- Dippery, J. K., Tissue, D. T., Thomas, R. B., and Strain, B. R.** (1995). Effects of low and elevated CO₂ on C₃ and C₄ annuals. I. Growth and biomass allocation. *Oecologia* **101**, 13–20.
- Hocking, P. J., and Meyer, C. P.** (1991). Effects of CO₂ enrichment and nitrogen stress on growth and partitioning of dry matter and nitrogen in wheat and maize. *Australian Journal of Plant Physiology* **18**, 339–356.
- Johnson, I. R.** (1985). A model of partitioning of growth between the shoots and the roots of vegetative plants. *Annals of Botany* **55**, 421–431.
- Kuehny, J. S., Peet, M. M., Nelson, P. V., and Willits, D. H.** (1991). Nutrient dilution by starch in CO₂-enriched *Chrysanthemum*. *Journal of Experimental Botany* **42**, 711–716.
- Lefebvre, D. D., and Glass, A. D. M.** (1982). Regulation of phosphate influx in barley roots: effects of phosphate deprivation and reduction of influx with provision of orthophosphate. *Physiologia Plantarum* **54**, 199–206.
- Lowther, J. R.** (1980). Use of a single sulfuric acid–hydrogen peroxide digest for the analysis of *Pinus radiata* needles. *Communications in Soil Science and Plant Analysis* **11**, 175–188.
- McKee, I. F., and Woodward, F. I.** (1994). CO₂ enrichment response of wheat: interaction with temperature, nitrate and phosphate. *New Phytologist* **127**, 447–453.
- Norby, R. J.** (1994). Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. *Plant and Soil* **165**, 9–20.
- Norby, R. J., O'Neill, E. G., Hood, W. G., and Luxmoore, R. G.** (1987). Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO₂ enrichment. *Tree Physiology* **3**, 203–210.
- Nye, P. H., and Tinker P. B.** (1977). 'Solute Movement in the Soil–Root System.' (Blackwell Scientific Publishers: Oxford.)
- O'Neill, E. G., Luxmoore, R. J., and Norby, R. J.** (1987). Elevated atmospheric CO₂ effects on seedling growth, nutrient uptake, and rhizosphere bacterial population of *Liriodendron tulipifera* L. *Plant and Soil* **104**, 3–11.
- Patterson, D. T., Flint, E. P., and Beyers, J. L.** (1984). Effects of CO₂ enrichment on competition between a C₄ weed and a C₃ crop. *Weed Science* **32**, 101–105.
- Reynolds, J. F., Virginia, R. A., and Schlesinger, W. H.** (1996). Defining functional types for models of desertification. In 'Functional Types'. (Eds T. M. Smith, H. H. Shugart and F. I. Woodward.) pp. 194–214. (Cambridge University Press: Cambridge.)
- Robinson, D.** (1986). Compensatory changes in the partitioning of dry matter in relation to nitrogen uptake and optimal variation in growth. *Annals of Botany* **58**, 841–848.
- Rogers, G. S., Milham, P. J., Gillings, M., and Conroy, J. P.** (1996). Interaction between rising CO₂ concentration and nitrogen supply in cotton. I. Growth and leaf nitrogen concentration. *Australian Journal of Plant Physiology* **23**, 119–125.
- Rogers, H. H., Runion, G. B., and Krupa, S. V.** (1994). Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution* **83**, 155–189.
- Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Hueneke, L. F., Jarrell, W. M., Virginia, R. A., and Whitford, W. G.** (1990). Biological feedbacks in global desertification. *Science* **247**, 1043–1048.
- Siddiqi, M. Y., Glass, A. D. M., Ruth, T. J., and Ruffy, T. W.** (1990). Studies of the uptake of nitrate in barley. I. Kinetics of ¹³N₃⁻ influx. *Plant Physiology* **93**, 1426–1432.
- Sinclair, T. R.** (1992). Mineral nutrition and plant growth response to climate change. *Journal of Experimental Botany* **43**, 1141–1146.
- Sokal, R. R., and Rohlf, F. J.** (1981). 'Biometry.' (W. H. Freeman: San Francisco.)
- Stulen, I., and den Hertog, J.** (1993). Root growth and functioning under atmospheric CO₂ enrichment. *Vegetatio* **104/105**, 99–115.
- Thomas, R. B., and Strain B. R.** (1991). Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiology* **96**, 627–634.
- Tschaplinski, T. J., Norby, R. J., and Wullschleger, D. S.** (1993). Responses of loblolly pine seedlings to elevated CO₂ and fluctuating water supply. *Tree Physiology* **13**, 283–296.
- Vessey, J. K., Henry, L. C., and Raper Jr., C. D.** (1990). Nitrogen nutrition and temporal effects of carbon dioxide on soybean growth. *Crop Science* **30**, 287–294.
- Wong, S. C.** (1979). Elevated atmospheric partial pressure of CO₂ and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C₃ and C₄ plants. *Oecologia* **44**, 68–74.
- Wray, S. M., and Strain, B. R.** (1987). Competition in old-field perennials under CO₂ enrichment. *Ecology* **68**, 1116–1120.

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