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8

Response of Plants to Elevated Atmospheric CO_2: Root Growth, Mineral Nutrition, and Soil Carbon

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I. CO_2 Response

The rise in atmospheric CO_2, due mainly to fossil fuel combustion and land use change, is an undisputed fact. This ongoing CO_2 increase has important implications for vegetation. Plant growth is typically enhanced by elevated CO_2. Carbon dioxide is the substrate for photosynthesis and, when elevated, both carbon assimilation and water use efficiency generally increase. Stimulation of root system development associated with increased growth implies more rooting, which, in turn, implies the possibility of increased water and nutrient capture. Microbes mediate C and nutrient flows within the soil, and CO_2-induced changes in the structure and function of plant root systems may lead to changes in the microbiology of both rhizosphere and soil. Enhanced plant growth further suggests greater delivery of C to soil, and thus potentially greater soil C storage. Soil is a vital reservoir in the global C cycle. Sequestration of soil C is closely linked to nutrient cycling. Root growth, rhizosphere microbiology, nutrient cycling and availability, and C storage in soils are integrally linked (Fig. 1; Zak *et al.*, 1993) and have important implications for plant health. Predicting how belowground processes respond to rising CO_2 will be necessary for the management of future crop and forest systems.

II. Roots

Effects of atmospheric CO_2 concentration on belowground processes have recently received increased attention within the research community,

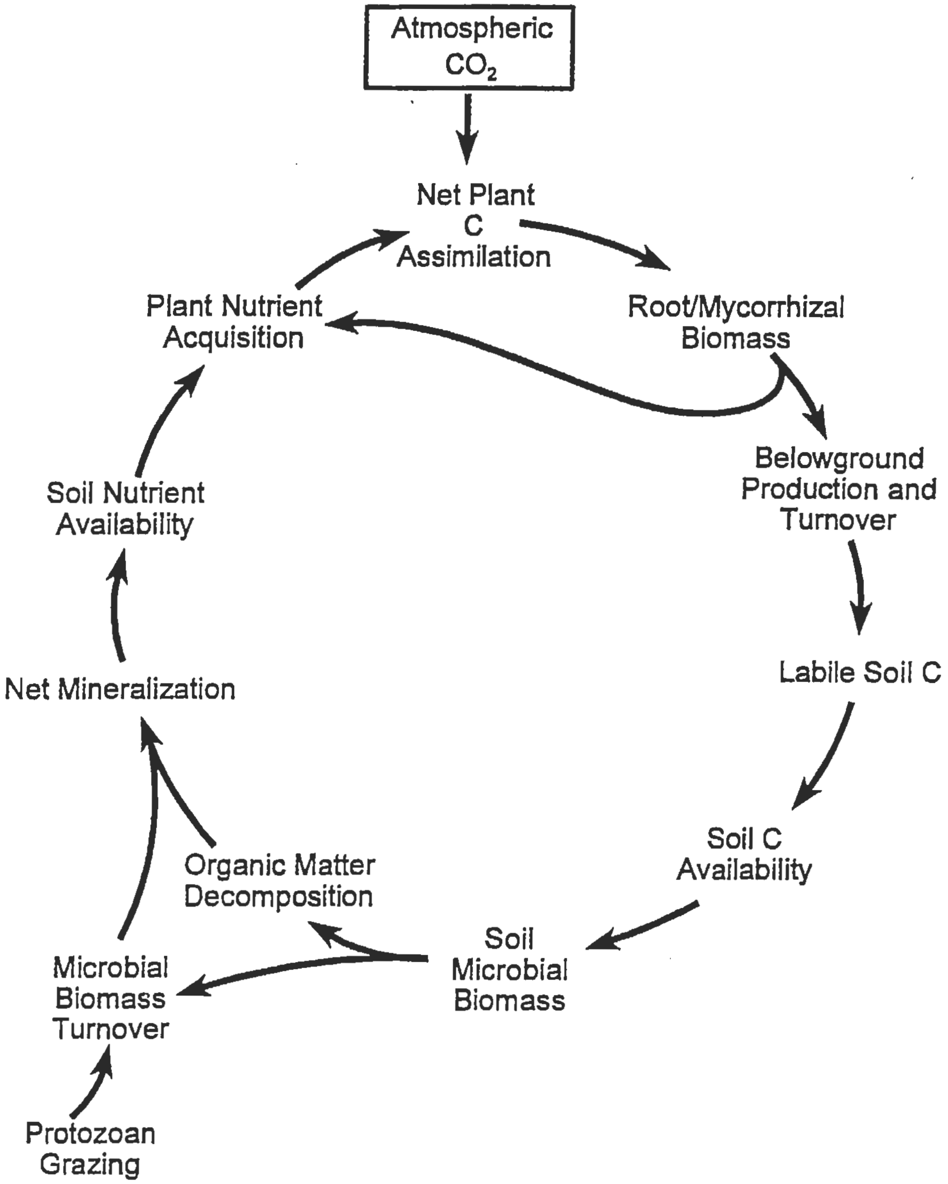

Figure 1 A conceptual model depicting the influence of elevated atmospheric CO_2 on plant production, microbial activity, and the cycling of C and nutrients. The model is characterized by a series of positive feedbacks in which increased net carbon assimilation under elevated CO_2 results in increased fine root/mycorrhizal growth, microbial biomass, and rate of nutrient mineralization. (Adapted with permission from Zak *et al.*, 1993.)

particularly with regard to root growth. Luo *et al.* (1994) have developed an excellent framework for predicting response of photosynthesis and root fraction to CO_2 enrichment which includes the interaction of C, N, and growth. They found that the response of the root fraction tends to rise or fall if photosynthesis is more sensitive to changes in CO_2 concentration than to relative growth rate. Apparently, this is often the case, because raising the CO_2 level frequently leads to increased root growth.

Rogers *et al.* (1992a) demonstrated enhanced root growth in soybean [*Glycine max* (L.) Merr.]. Root dry weight, length, diameter, and volume increased when CO_2 was elevated; however, total root number exhibited no response. Del Castillo *et al.* (1989) found that soybean root weight was approximately 28% higher in CO_2-enriched chambers and that cumulative root length correspondingly increased; no effect on rate of root elongation was seen. However, there was a linear increase in number of actively growing roots, that is, root systems were more branched. They concluded that roots of soybean plants growing under high concentrations of CO_2 would not explore a greater volume of soil, but would explore a given volume more thoroughly. These results contrast with Rogers *et al.* (1992a), who found a 110% increase in root length of soybean with no change in number of lateral roots.

Chaudhuri *et al.* (1990) found that winter wheat (*Triticum aestivum* L.) under elevated CO_2 achieved maximum rooting depth faster than in ambient air. Differences in root growth occurred primarily in the upper 10 cm of the soil profile, and they concluded that high CO_2 could compensate for restricted root growth brought about by drought, particularly in this top 10 cm of soil. With [*Sorghum bicolor* (L.) Moench], Chaudhuri *et al.* (1986) found that numbers and dry weights of roots were higher at all soil profile depths (to 150 cm) under elevated CO_2.

Belowground responses have been observed in cotton (*Gossypium hirsutum* L.) under free-air CO_2 enrichment (Rogers *et al.*, 1992b; Prior *et al.*, 1994a,b, 1995). Dry weights, lengths, and volumes of taproots, lateral roots, and fine roots were often higher for CO_2-enriched cotton plants. Although the numbers of lateral roots per unit length of taproot tended not to be increased by elevated CO_2, the overall greater taproot lengths under CO_2 enrichment usually had increased total numbers of laterals. Fine root patterns within the soil profile were also investigated; vertical and horizontal distributions of fine root density per unit volume of soil (expressed as length or dry weight m^{-3}) were measured. Although rooting was most pronounced in the upper 45 cm of the soil profile, the density of fine roots was seen to increase under CO_2 enrichment at most depths to 90 cm. Root length and dry weight densities also tended to exhibit greater differences between ambient and elevated CO_2 treatments with horizontal distance from row center, indicating a faster and more prolific spread of cotton roots. The location and density of roots within the soil profile is particularly important in that it determines nutrient acquisition, especially for ions with low diffusivity such as phosphate (Barber and Silberbush, 1984; Ikram, 1990; Caldwell *et al.*, 1992).

Highly significant increases in the growth of corms and roots of the C_3 tropical konjak (*Amorphophallus konjac* K. Koch) have been observed (Imai and Coleman, 1983); doubling CO_2 concentration doubled corm yield. In a separate study (Imai *et al.*, 1984), a large increase in growth (150%) was measured for the tropical root crop cassava (*Manihot esculenta* Crantz), with greater partitioning to roots. Carbon dioxide also causes large gains in root dry weight in rice (*Oryza sativa* L.) (Ziska and Teramura, 1992).

Adding CO_2 to greenhouses with mist systems raised the percentage of cuttings that formed roots in numerous horticultural species (Lin and Molnar, 1981; French, 1989). Elevating CO_2 during propagation also increased root number and length in sweet potato [*Ipomoea batatas* (L.) Lam.] (Bhattacharya *et al.*, 1985). Laforge *et al.* (1991) saw increases in root dry weight and root number of raspberry (*Rubus idaeus* L.) plantlets under high CO_2. Davis and Potter (1983) reported increases in root length and dry weight for several ornamentals, but root number increased only for *Peperomia glabella* A. Dietr. 'Variegata.' In further work with leafy pea (*Pisum sativum* L.) cuttings, elevated CO_2 increased carbohydrates, water potential, and root system size, but not root number (Davis and Potter, 1989). However, Grant *et al.* (1992) suggested that improved rooting was due to better water relations rather than increased carbohydrate levels.

There have been few studies on natural ecosystems. In a field study of elevated CO_2 effects on a Chesapeake Bay salt marsh, Drake (1992) noted increased numbers of roots and rhizomes (with increased allocation of C to them) for the C_3 sedge, *Scirpus olneyi* A. Gray. Investigations of a tallgrass prairie ecosystem (Owensby *et al.*, 1993b) have demonstrated increased root biomass for some species that may have led, at least in part, to shifts in species composition. Billings *et al.* (1984) concluded from vegetation/soil core studies that net production in tundra ecosystems was unlikely to be directly affected by CO_2 even at twice the ambient value. Indirect effects of CO_2 that could possibly become important in the tundra were temperature, water table, peat decomposition, and soil nutrient availability.

Berntson and Woodward (1992) reported that elevated CO_2 and water stress resulted in root foraging, branching patterns, and root lengths that resembled adequately watered, ambient CO_2-grown *Senecio vulgaris* L. plants, implying possible alleviation of stress. Prior *et al.* (1997) reported similar findings for longleaf pine (*Pinus palustris* Mill.). Root biomass of water-stressed seedlings increased (110%) when grown under elevated CO_2 conditions; elevated CO_2 also increased total fine root length for seedlings under water-stressed conditions.

Root response to CO_2 is influenced by interacting treatment conditions and, in their recent review, Stulen and den Hertog (1993) attributed experimental variability in root response (growth and function) to differential treatment of plants (i.e., water, nutrients, and pot size). They concluded that more CO_2 research on belowground effects is required and that the root to shoot ratio (R:S) effect needs critical reexamination. We have recently reviewed both belowground responses to CO_2 enrichment and the effects of elevated CO_2 on R:S.

In an examination of 167 studies of root response to CO_2 enrichment (Rogers *et al.,* 1994), root dry weight was the most frequently examined root measure and was included in about 50% of the studies. Most of these investigations (≈87%) found increases in root dry weight under elevated atmospheric CO_2, regardless of species or study conditions. Further, roots often exhibited the greatest relative dry weight gain, among tissues, for plants exposed to high CO_2 (Imai and Murata, 1976; Wittwer, 1978; Rogers *et al.,* 1983; Imai *et al.,* 1985; Hocking and Meyer, 1991b; Norby *et al.,* 1992). A majority (77%) of the studies in our survey (Rogers *et al.,* 1994) found that elevated CO_2 resulted in more and/or longer plant roots, possibly leading to increased spread (Idso and Kimball, 1991, 1992) and/or penetration of the soil profile (Baker *et al.,* 1990; Rogers *et al.,* 1992b).

Tognoni *et al.* (1967) reported the general promotion of root growth by higher levels of CO_2 with accompanying increases in R : S. However, despite fairly consistent results with most root measures, R : S responses have been more variable. For example, Laforge *et al.* (1991) reported an approximate doubling of R : S for raspberry plantlets and Rogers *et al.* (1992a) reported an increase in soybean R : S under high CO_2; while Chu *et al.* (1992) studying wild radish (*Raphanus sativus x raphanistrum* L.) and Prior *et al.* (1994a) working with cotton grown under field conditions reported that R : S was unaffected by CO_2 treatment. Further, in one study of 27 herbaceous species, R : S decreased in 14 species, increased in 6 species, and was unaffected in 7 species under elevated CO_2 (Hunt *et al.,* 1991).

In our examination of root response to CO_2 enrichment (Rogers *et al.,* 1994), R : S increased in agronomic (88% of studies), forest (86%), and natural community (81%) species; however, a wide range was seen in R : S among species and among study conditions. More recently, we have identified 264 determinations of R : S response in crop species under elevated atmospheric CO_2 (Rogers *et al.,* 1996), which adds further support to the contention that the response of R : S to elevated atmospheric CO_2 is highly variable among crop species and experimental conditions. Positive responses in R : S to elevated CO_2 occurred in 59.5% of these reports, while negative responses occurred in 37.5%, and no response occurred 3.0% of the time. We, in fact, found that the response of R : S to increased concentrations of atmospheric CO_2 approximates a normal distribution (Rogers *et al.,* 1996). Further analysis demonstrated that, while most of these observations were clustered close to zero (75.4% occurred between ±30%), there was a mean positive response (+11.1%), which was statistically greater than zero. This increase in R : S was found to be in general agreement with other reviews in the CO_2 literature (Acock and Allen, 1985; Enoch and Zieslin, 1988; Norby *et al.,* 1995; Wullschleger *et al.,* 1995).

In addition to the four primary variables (root dry weight, R : S, root length, and root number), other root responses to elevated atmospheric

CO_2 have been observed. Examination of structural aspects of roots (i.e., diameter, volume, branching, and relative growth rate) have usually shown positive effects of high CO_2. Tubers (number, dry weight, and diameter) and nodulation (number, dry weight, and activity) also benefit from elevated CO_2 in most cases (Rogers *et al.,* 1994). In a summary of available data, Porter and Grodzinski (1985) reported a mean yield ratio (for high CO_2) of 1.40 for mature root crops and of 1.77 for immature root crops.

Other root factors seen to increase with CO_2 (though infrequently examined) include parenchyma cell division and expansion, mycorrhizae, and carbohydrate levels (Rogers *et al.*, 1994). Results of Ferris and Taylor (1994), using a biophysical analysis of root cell elongation as influenced by elevated CO_2 suggested that root growth is stimulated after increased cell expansion. Indications were that increased P and cell wall tensiometric extensibility are probably both key to enhanced root growth of plants in elevated CO_2. Time to harvest (though seldom reported) was found to be shortened for root and tuber crops (Cummings and Jones, 1918).

Available literature demonstrates that, while responses may vary among species and study conditions, more CO_2 tends to result in positive, sometimes dramatic, responses in the belowground portion of plants. Increased rooting has the potential to alter significantly the edaphic environment through increased C deposition and/or nutrient uptake by plants; this may have important consequences for managed and natural terrestrial ecosystems, particularly under potentially changing climates. However, increased C storage in soil depends not only on the quantity and quality of C deposited, but also on the manner and speed with which it is recycled once on or in the soil (Fig. 1). Similarly, increased resource acquisition from soil depends not only on the ability of roots to forage for nutrients, but also on the accessibility and availability of these nutrients. Effects of CO_2 on these processes will largely depend on how rhizosphere and soil microorganisms respond.

III. The Rhizosphere

Carbon dioxide-induced changes in plants will affect the structure (species populations) and function (activity) of rhizosphere and soil microorganisms. As pathogens, symbionts, and decomposers, microbes exert a strong influence on C and nutrient cycling in plant/soil systems (Fig. 1). Changes in plant structure (Thomas and Harvey, 1983; Prior *et al.*, 1995), physiology (Amthor, 1991; Rogers and Dahlman, 1993; Amthor *et al.*, 1994; Rogers *et al.*, 1994), and phytochemistry (Melillo, 1983; Lekkerkerk *et al.*, 1990; Liljeroth *et al.*, 1994; Pritchard *et al.*, 1997) brought about by elevated atmospheric CO_2 may alter plant–microbe interactions and, thus, plant health and C and nutrient cycling in the soil.

Despite the potential for increasing CO_2 (through changes in growth, exudation, and tissue chemistry) to alter interactions of plant roots with pathogenic microbes, this area remains virtually unstudied. Runion *et al.* (1994) reported a trend for increased infestation of root-zone soil of cotton by *Rhizoctonia* spp., under free-air CO_2 enrichment (FACE). Although this suggested the potential for elevated CO_2 to increase root disease, a bioassay using this soil demonstrated no increase in damping-off potential. Additionally, they reported a trend for lower numbers of parasitic nematodes under FACE, which they related to increased competition from a larger population of saprophagous nematodes (Runion *et al.*, 1994).

It has been hypothesized that, due to additional C entering plant rhizospheres, atmospheric CO_2 enrichment could result in greater mycorrhizal colonization of roots (Luxmoore, 1981; Lamborg *et al.*, 1983). This potential increase in mycorrhizal colonization could benefit host plants via increased nutrient (Bowen, 1973; Tinker, 1984) or water (Bowen, 1973; Augé *et al.*, 1987) uptake and by protecting roots from adverse edaphic conditions such as temperature extremes, high salinity, or pathogenic microorganisms (Marx, 1973; Duchesne, 1994). The fact that mycorrhizae can provide additional water to plants through hyphal proliferation in soil (Luxmoore, 1981) might explain, in part, observed increases in biomass of CO_2-enriched plants under drought stress. These beneficial effects of mycorrhizae could, then, increase plant productivity, leading to greater amounts of organic matter supplied to the soil.

Carbon dioxide enrichment has been reported to increase mycorrhizal colonization in roots of several plant species (Norby *et al.*, 1987; O'Neill *et al.*, 1987b; Monz *et al.*, 1994; Runion *et al.*, 1997) or, even in the absence of an effect on a unit root length basis, to increase numbers of mycorrhizae on a whole-plant basis due to significant increases in total root length (Norby *et al.*, 1986a; O'Neill *et al.*, 1991; Runion *et al.*, 1994). Runion *et al.* (1997) suggested that sink/source relationships may be a major factor regulating mycorrhizal development in high-CO_2 environments. That is, when either photosynthate supply is not source limited (elevated CO_2) or when tissue N concentrations are low (elevated CO_2 or low soil N), plants alter allocation to soil resource acquisition by investing in roots and mycorrhizae. Lewis *et al.* (1994b) found that, for loblolly pine (*Pinus taeda* L.) from different geographic sources, mycorrhizal colonization responded differentially to CO_2 enrichment. For two pines (*Pinus radiata* D. Don and *P. caribaea* P.M. Morelet var. *hondurensis*), elevated CO_2 boosted P uptake when soil P availability was low (Conroy *et al.*, 1990b); changes in mycorrhizae appeared to be the most probable cause. It was concluded that high leaf P concentrations would be necessary if the full potential for more atmospheric CO_2 on pine forests were to be realized.

Study of N fixation (the incorporation of atmospheric N into nitrogenous compounds which can be utilized by living organisms) as influenced by atmospheric CO_2 has generally shown that legume/bacterial symbiosis is favored by elevated CO_2 (Reddy *et al.,* 1989; Reardon *et al.,* 1990). Acock (1990) concluded that the positive effect of CO_2 on N fixation appeared to be simply the result of more biomass. This is supported by work showing that, when atmospheric CO_2 is high, nodule dry weight increases but specific nodule activity (g N g^{-1} nodule) does not (Williams *et al.,* 1981; Finn and Brun, 1982). However, others have found increases in nodule activity under CO_2 enrichment (Hardy and Havelka, 1973; Whiting *et al.,* 1986; Norby and Sigal, 1989) and relate the increased activity to photosynthetic stimulation. These differing results may be due to differences in plant species (Masuda *et al.,* 1989a,b), experimental conditions, or duration of CO_2 exposure. Phillips *et al.* (1976) obtained results indicating that long-term enrichment promoted fixation by enhancing nodule development in peas, while short-term high-CO_2 exposures increased fixation by affecting nodule function. In their work with white clover (*Trifolium repens* L.), Masterson and Sherwood (1978) found that the expected decrease in N fixation at high levels of soil N did not occur under elevated CO_2. Allen *et al.* (1991) observed a positive effect of high CO_2 on N-fixing soil bacteria, which improved N nutrition and yield of rice.

In addition to their effects as symbionts, soil microorganisms are responsible for the decomposition of organic matter; through the processes of decomposition and mineralization, nutrients become available to plants (Grant and Long, 1981; Paoletti *et al.,* 1993). Not only can soil and rhizosphere microbes make nutrients available to plants, they can also make them unavailable through immobilization. In an experiment with labeled plant residues, Jenkinson (1966) found that about 35% of labeled C remaining in the soil after 1 yr was present as microbial biomass. Soil microfauna (e.g., nematodes and microarthropods) are also important in nutrient cycling (Coleman *et al.,* 1984; Freckman, 1988; Ingham, 1988; Rabatin and Stinner, 1988; Runion *et al.,* 1994).

In many terrestrial ecosystems, nutrients are a primary factor limiting plant growth; however, nutrient uptake and plant growth are not usually related to the total nutrient content of the soil, but rather to the quantity of nutrients mineralized by microbes and available for plant growth (Grove *et al.,* 1988). For example, microbial transformations of organic P often produce the majority of the plant available solution P (Paul and Voroney, 1980).

Zak *et al.* (1993) saw a positive feedback between C and N soil dynamics and elevated CO_2 (Fig. 1) using *Populus grandidentata* Michx. grown on nutrient-poor soil. They reported significant increases in microbial biomass C in the rhizosphere and in bulk soil associated with plants grown under elevated CO_2. They also observed greater N mineralization, which was possibly related to both increased turnover of microbial N and release of N from soil organic matter. O'Neill *et al.* (1987a) found that, while nitrite-oxidizing and phosphate-dissolving bacteria in the rhizosphere of yellow poplar (*Liriodendron tulipifera* L.) seedlings were reduced at the final harvest, total N and P uptake were increased under high CO_2. They speculated that the decline in bacteria populations was a function of decreased nutrient availability due to increased competition with seedling roots as the growing season progressed. Runion *et al.* (1994) found that, while dehydrogenase activity (a measure of microbial respiration) was significantly higher in soils from CO_2-enriched cotton plants, no appreciable differences in microbial populations (fungi, bacteria, and actinomycetes) were observed.

Elevated CO_2-induced changes in plant tissue quantity and quality can affect the composition and activity of rhizosphere and soil microbes and thus impact C turnover and storage in soils (Goudriaan and de Ruiter, 1983; Lamborg *et al.*, 1983). Overdieck and Reining (1986) raised the possibility of slowing decomposition rates by increased C:N ratios in high-CO_2 grown plants. Such an effect could slow the cycling of both C and nutrients, and thus reverse the positive CO_2 effect on vegetation in the long run. Melillo (1983) reported higher C:N ratios and higher levels of phenolics in sweetgum leaves exposed to high CO_2 and hypothesized that this would result in reduced decomposition rates and decreased soil fertility. Ball (1992) found decreased growth of lignocellulose-degrading actinomycetes on elevated CO_2-grown wheat material, resulting in reduced degradation, which was related to increased lignification and changes in the C:N ratio. Lekkerkerk *et al.* (1990) found that the input of easily decomposable root-derived material in soil supporting wheat plants was increased and, due to microbial preference for these materials, turnover of more resistant soil organic matter was reduced under elevated CO_2. Coûteaux *et al.* (1991) demonstrated similar results for an initial decomposition period and related the reduction in decomposition rate to lower N concentration and higher C:N ratios of CO_2-enriched plants. However, when they allowed decomposition to continue, changes in the composition of the decomposer population (increase in microfauna and introduction of white-rot fungi) resulted in an increased decomposition rate of material (produced under CO_2 enrichment) while the rate for control materials declined. These CO_2-induced shifts in decomposer composition led to an overall 30% rise in C mineralization. An increase in C turnover was also observed in soils where CO_2-enriched cotton plants had grown for three seasons (Wood *et al.*, 1994) and could be related to increases in soil microfauna and saprophagous nematode populations (Runion *et al.*, 1994).

Elevated atmospheric CO_2, acting through plant-mediated changes in the quantity and quality of organic materials entering the rhizosphere, may alter the composition and activity of soil microbes. Increasing atmospheric CO_2 may negatively affect pathogenic soil microbes and, thus, decrease root diseases, but this possibility has not been studied. In contrast, CO_2 effects on beneficial microorganisms (mycorrhizal fungi and N-fixing bacteria) have received more attention and enhanced plant health through increased interactions with microbial symbionts under CO_2 enrichment appears likely. Stimulation of N fixation and nutrient release by increased microbial (including mycorrhizal) and root activity are possible mechanisms that could raise fertility levels (Brinkman and Sombroek, 1996). Thus, rhizosphere and soil microbes may also improve plant health under CO_2 enrichment by increasing nutrient cycling and availability and by improving soil quality through increased C storage; however, generalizations regarding these effects cannot yet be made and further study is required.

IV. Mineral Nutrition

Mineral nutrition is essential to plant growth (Shuman, 1994; Marschner, 1995) and is therefore an important aspect of the CO_2 response. As Wolfe and Erickson (1993) have stated, "An accurate assessment of the effects of CO_2-doubling on crop productivity will require more information regarding complex interactions between CO_2 and nutrient availability, and a better understanding of how specific nutrient deficiencies influence plant response to CO_2." There is uncertainty associated with interactions between atmospheric CO_2 concentration and mineral nutrition (Sinclair, 1992) since complex interactions between roots and nutrients depend on the specific nutrient, its concentration, form when applied, and environmental conditions (Sattelmacher *et al.*, 1993).

A review of the literature for the past decade revealed that, while the absolute magnitude of plant growth is greater under adequate resource availability, the relative response to elevated CO_2 is generally enhanced most when resource limitations and environmental stresses are greatest (Idso and Idso, 1994). Although higher CO_2 levels may contribute to the plant's capacity to grow under nutrient deficient conditions, it is important to note this is not always the case. It has been suggested that larger root systems, higher photosynthetic rates, and greater activity in the rhizosphere may help overcome nutrient stress (Rogers *et al.*, 1994). In addition, root exudation, which can increase in plants grown under CO_2 enrichment (Norby *et al.*, 1987), might enhance nutrient acquisition, especially under stress conditions (Uren and Reisenauer, 1988).

Nitrogen and P are the nutrients most likely to be influenced by rising CO_2 since relatively high quantities of both are needed in the photoreductive C cycle and the photo-oxidative cycle (Rogers *et al.*, 1993; Gifford, 1992). Research has revealed that CO_2 enrichment will induce the greatest productivity in C_3 plants when soil N and P availability are high; that low N does not always eliminate the CO_2 growth effect; and that some species do not respond when P is insufficient, owing to a lessening of photosynthetic activity (Conroy *et al.*, 1986a,b; 1988; 1990a,b; 1992; Conroy, 1992; Conroy and Hocking, 1993). In general, maximum productivity under CO_2 enrichment requires higher tissue P concentrations, but the N requirement is reduced (Conroy, 1992). Rogers *et al.* (1993) reported that critical leaf N concentration was decreased while critical P level was increased in wheat and cotton grown under high CO_2. Duchein *et al.* (1993) demonstrated that supplying supraoptimal levels of P to clover (*Trifolium subterraneum* L.) exposed to high CO_2 greatly improved growth. However, Seneweera *et al.* (1994) reported that P level for maximum yield of rice was the same at both ambient and twice ambient CO_2. Lewis *et al.* (1994a) showed that P availability and photosynthetic capacity of loblolly pine were influenced by CO_2 level. Although long-term exposure to elevated CO_2 may reduce P stress, the authors point out that, in the field where P is already only marginally sufficient, plants could soon become P limited as global CO_2 level rises. Collectively, the above results imply that critical nutrient concentrations (those that promote maximum productivity) may need to be reconsidered in light of the rising level of atmospheric CO_2 (Hocking and Meyer, 1991a; Conroy *et al.*, 1992).

The essential need for nitrogen has made it a frequent target of research. Kimball and Mauney (1993) saw no interaction between CO_2 and soil N in cotton. Similarly, Wong (1979) reported reduced dry weight and leaf area for both maize (*Zea mays* L.) and cotton under low N supply at both ambient and elevated CO_2. Recently compiled literature on forest responses (Wullschleger *et al.*, 1997) also suggests that limited supplies of N, P, and water will only slightly inhibit tree growth response to CO_2 enrichment. This is supported by the work of Samuelson and Seiler (1993) who concluded that response of red spruce (*Picea rubens* Sarg.) to CO_2 rise may proceed even if water and nutrients are in short supply, and by Cure *et al.* (1988) who showed that atmospheric CO_2 enrichment can enhance yield of non-nodulating soybean even if N availability is limiting. In contrast, Bowler and Press (1993) showed no growth effect of elevated CO_2 in *Nardis stricta* L. at low N, but an increase in growth at high N; similar results have also been reported for loblolly (Griffin *et al.*, 1993) and longleaf pine (Prior *et al.*, 1997). Likewise, Wong *et al.* (1992) saw a positive interaction of CO_2 and N on dry weight and leaf area in four species of eucalyptus. Brown and Higginbotham (1986) reported that spruce [*Picea glauca* (Moench)

Voss] biomass was increased by high CO_2 at high N; aspen (*Populus tremuloides* Michx.) biomass also increased initially but this effect did not persist, suggesting development of a nutrient limitation as the plants grew. In contrast, Wong and Osmond (1991) found that wheat shoot growth was stimulated more in low than in high nitrate when subjected to elevated CO_2. Bowler and Press (1993) showed a proportionally greater growth response to high CO_2 at low compared with high N (78 and 58%, respectively) for the upland grass species, *Agrostis capillaris* L. These variable results suggest a need for further research.

Interacting effects of CO_2 and N on plant growth may be related to effects on photosynthesis, and changes in N supply will influence the photosynthetic response to CO_2 in a complex fashion (Woodward, 1992). In loblolly pine, photosynthetic rate showed similar responses to CO_2 and N as did growth; that is, rates of photosynthesis were higher at elevated CO_2 only when supplemental N was provided (Tissue *et al.,* 1993). However, increased photosynthesis in longleaf pine tended to occur under elevated CO_2 regardless of N fertility level (G. B. Runion, unpublished data). Bunce (1992) also showed that photosynthetic adjustment to elevated CO_2 in soybean and sugar beet (*Beta vulgaris* L.) was unaltered by increasing nutrient supply.

In addition to variability from differing levels of N, the source of this N can also influence response to CO_2. Carbon dioxide enhancement of photosynthetic rate in carob (*Ceratonia siliqua* L.) was proportionally higher than biomass increase when nitrate, rather than ammonium was the N source (Cruz *et al.,* 1993); the preferred N source was ammonium at both CO_2 levels. Also, carob grown with nitrate had higher sucrose content, while those on ammonium had greater starch storage. BassiriRad *et al.* (1996) observed that elevated CO_2 enhanced root uptake capacity for nitrate, but not for ammonium in loblolly pine. Substantially higher carbohydrate levels in roots were noted without a significant change in root N concentration. Elucidating the preferred form of nutrients will contribute to understanding the relationship of CO_2 to mineral cycling in the field. Clarifying this relationship will allow the development of better models and more accurate predictions. One forest modeling effort has suggested that decreases in foliar concentration of N could slow rates of N cycling between vegetation and the soil, and lower rates of N loss through gaseous emission, fire, and leaching (Comins and McMurtrie, 1993). It was revealed that in the long term the equilibrium elevated CO_2 response would be sensitive to the rate of gaseous N loss due to mineralization. Another interesting aspect of greater nutrient capture by plant root systems is the possibility of a shift in the N cycle where more N is held in organic form within CO_2-enriched agro-ecosystems, leading to improved groundwater quality (Torbert *et al.,* 1996).

Some research has examined responses to elevated CO_2 under generalized nutrient regimes, and again results have been variable. Sionit (1983) found that limited nutrient supply in soybean could be at least partially ameliorated by CO_2 enrichment and reported that yield response to high CO_2 rose significantly at the highest nutrient level, suggesting a need for more fertilization. Sionit *et al.* (1981) reported that total dry matter of wheat increased with elevated CO_2 regardless of nutrition level (1/16, 1/8, 1/2, and full-strength Hoagland's solution); for ambient CO_2, yield increased up to the 1/2 strength level, but fell at full strength. Patterson and Flint (1982) reported growth enhancement by CO_2 in soybean, sicklepod (*Cassia obtusifolia* L.), and showy crotalaria (*Crotalaria spectabilis* Roth) at both 1/8 and 1/2 strength Hoagland's solution. Newbery (1994) observed no interaction between nutrient supply and elevated CO_2 for *Agrostis capillaris.* Norby and O'Neill (1991) also reported whole plant and root dry weight increases in yellow poplar with and without added mineral nutrients. Growth of bean (*Phaseolus vulgaris* L.) was also positively affected with or without adequate nutrition (Radoglou and Jarvis, 1992). In contrast to this lack of response to nutritional level, McKee and Woodward (1994) found that CO_2 enhancement of spring wheat was limited by low nutrient supplies. Similarly, Curtis *et al.* (1995) observed greater dry weight gain in hybrid poplar [*Populus x euramericana* (Dode) Guinier cv. Eugenia] exposed to twice ambient CO_2 at high (49%) compared with low (25%) fertility levels. They also found that photosynthetic capacity in the high-CO_2 treatment fell off more rapidly for the low fertility plants (100 days) than for those at high fertility (135 days). Bazzaz and Miao (1993) reported that the greatest stimulation in growth by CO_2 enrichment for six tree species (*Betula alleghaniensis* Britton, *B. populifolia* Marsh., *Fraxinus americana* L., *Acer rubrum* L., *A. pennsylvanicum* L., and *Quercus rubra* L.,) occurred under high nutrient conditions; further, the three early successional species (*B. populifolia, F. americana,* and *A. rubrum*) showed significant growth increases only in the high nutrient regime. In sweet chestnut (*Castanea sativa* Mill), soil nutrient availability caused a shift in partitioning with CO_2 enrichment (El Kohen *et al.,* 1992); root dry weight increased in unfertilized soil, while only stem dry weight increased with fertilization.

Interactions of CO_2 and nutrients have primarily focused on effects on biomass (production and allocation) and/or photosynthesis. However, other physiological parameters of interest have been examined. Radoglou *et al.* (1992) observed that, while water use efficiency (WUE) of bean plants showed a linear increase over the CO_2 concentration range, WUE was doubled at a high nutrient and tripled at a low nutrient supply. Masle *et al.* (1992) also observed a positive correlation between WUE and leaf mineral content in several species. Coleman *et al.* (1993) suggested that decreases in plant N concentration may not be the result of a physiological change in N use efficiency, but rather a phenomenon dependent on plant size increase that occurs because CO_2 accelerates growth (which could affect water use). Conroy and Hocking (1993) suggest that, besides the diluting effect of extra C compounds, reduction in nutrient absorption might result from slower transpiration rates. Experiments by Ito (1970) raised the possibility that CO_2-induced reduction in transpiration would lower the uptake of P. In light of these findings, and the often reported increase in WUE by elevated CO_2, there is good reason to explore the interaction of CO_2 and mineral nutrition.

Results on nutrient uptake and concentration are variable due to differences in nutrient application during the course of the experiments (Linder and McDonald, 1993). For example, Israel *et al.* (1990) reported that, if plants growing under high CO_2 are supplied with higher levels of nutrients, tissue nutrient concentrations and nutrient uptake efficiency are generally not significantly affected by CO_2 concentration. On the other hand, it has been suggested that when plants are grown under nutrient levels considered poor to adequate for ambient conditions, high CO_2 results in larger plants with lower tissue nutrient concentrations (Norby *et al.*, 1986a,b; Yelle *et al.*, 1987; Silvola and Ahlholm, 1995). In fact, nutrient concentrations in plant parts are often lower under high CO_2 regardless of soil nutrient availability. For example, Reeves *et al.* (1994) observed lower tissue N concentrations in soybean (N-fixing) grown under elevated CO_2. Johnson *et al.* (1995) also saw dilution of tissue N concentration in ponderosa pine (*Pinus ponderosa* Douglas ex P. Laws. & C. Laws.) exposed to elevated CO_2, even when growing in high N soil; however, a more efficient use of internal N reserves was noted. El Kohen *et al.* (1992) found that, while the total N pool was unaffected by extra CO_2 tissue N concentration was reduced in sweet chestnut. A decline (approximately 25%) in leaf mineral content (N, P, K, Ca, and Mg) under high CO_2 has also been observed in bean (Porter and Grodzinski, 1984); carbohydrate dilution was suggested as the cause (Porter and Grodzinski, 1985). McKee and Woodward (1994) reported that high-CO_2 treatment reduced both the shoot N concentration and the proportional allocation of N to the uppermost leaves of spring wheat, which could impact photosynthesis. Thompson and Woodward (1994) found that, while CO_2 enrichment increased grain yield of spring wheat and spring barley (*Hordeum vulgare* L.), the grain N content was reduced, enough so that current bread-making procedures would be affected. Hocking and Meyer (1991b) saw higher nitrate reductase activity in wheat grown in high CO_2 with an accompanying increase in N use efficiency. Total N accumulated was greater but the increase did not rise in proportion to the CO_2-induced dry weight gain and, therefore, N concentration fell; similar results were reported for cocklebur (*Xanthium occidentale* Bertol.) (Hocking and Meyer, 1985).

Few studies have explored nutrient interactions *in situ,* within CO_2-enriched plant communities. In a 3-yr study of tallgrass prairie response to elevated CO_2, Owensby *et al.* (1993a) saw increased biomass of C_4 grasses. Total N content went up while tissue N concentration came down. The total N rise was attributed to enhanced root exploration of the soil profile by larger root systems. Enhanced P nutrition was also observed. Growth of C_3 species was not substantially increased, but tissue concentration of N was reduced as in the C_4 grasses. In a salt marsh community of three species growing under an approximate CO_2 doubling, Curtis *et al.* (1989) noted a substantial rise in C:N ratio for *Scirpus olneyi* (C_3), but no effect on two C_4 plants, [*Spartina patens* (Aiton) Muhl.] and [*Distichlis spicata* (L.) Greene]. Total aboveground N for *S. olneyi* remained unchanged, suggesting that the observed growth stimulation was dependent on reallocation of stored N. A lowering of decomposition rates as well as forage quality appeared to be probable consequences of the reduced N concentration. Woodin *et al.* (1992), investigating the effect of CO_2 on heather (*Culluna vulgaris* L.), observed that the total nutrients absorbed did not increase, thus tissue concentration fell. Their results suggested that heather, in its usually nutrient-poor habitats, would become nutrient limited by even small rises in atmospheric CO_2 level. Nutrient cycling is integrally linked to competition within natural communities. The effect of CO_2 on this cycling may alter competitive relationships, thereby changing community structure and function.

Although a decline in nutrient concentration of plant tissue under high CO_2 is the general rule, nutrient uptake is often increased by elevated CO_2; however, results have varied among species and among elements. Peñuelas and Matamala (1990) examined the N and S content of leaves in herbarium specimens of 14 species collected from 1450 to 1985. A significant overall decrease in N was seen. The S content showed no long-term trend, but a sharp upturn in the 1940s was attributed to the burning of high-sulfur coal during those years. In a similar study (Peñuelas and Matamala, 1993) of mineral content of 12 species (trees, shrubs, and herbs) during the last 250 yr, present levels of Al, Ca, Cu, Sr, Fe, P, Mg, Mn, K, Na, S, and Zn were found to be lower than at any other period. Larigauderie *et al.* (1994) noted greater N uptake rates for loblolly pine grown with high N supply, but lower uptake with low N supply, under high CO_2. Newbery (1994) observed that the uptake of N, P, and K did not increase proportionally with CO_2-induced increases in growth; K concentration declined, while N and P concentrations were similar for *Agrostis capillaris* plants grown with elevated CO_2 compared with those grown in ambient air. The large rise in K demand was suggested to have been related to shifts in osmoregulation. Seneweera *et al.* (1994) reported that leaf P content of rice was unaffected by CO_2 treatment over a range of added P (0–480 mg kg^{-1} as $CaHPO_4 \cdot 2H_2O$).

Luxmoore *et al.* (1986) saw increases in dry weight and uptake of N, Ca, Al, Fe, Zn, and Sr in Virginia pine (*Pinus virginiana* Mill.) under CO_2 enrichment. Greater uptake was associated with increased root weight. Specific absorption rates (uptake per unit root dry weight) were generally unaltered by high CO_2. Uptake of P and K did not increase with elevated CO_2, but had greater nutrient use efficiency. Nitrogen and Ca use efficiency were not affected. The rise in Zn uptake may have resulted from increased pH in the rhizosphere since, under elevated CO_2, cations were more readily absorbed than anions. Results suggested increased nutrient retention under high CO_2. O'Neill *et al.* (1987a) reported that, for yellow poplar, absorption of N, S, and B were lower at elevated CO_2, while uptake of Ca, Mg, Sr, Ba, Zn, and Mn remained uninfluenced by enrichment. Uptake of P, K, Cu, Al, and Fe was proportional to growth at both ambient and high CO_2. Wong *et al.* (1992), working with four eucalypts, saw increased N use efficiency under elevated CO_2 for both leaf and whole plant at low N. In the case of high N, leaf N use efficiency went up in two species, but went down in the other two species. Kuehny *et al.* (1991) noted nutrient dilution by CO_2 enrichment in *Chrysanthemum x morifolium* Ramat. cv. Fiesta. When corrected for leaf starch content, differences in N, P, K, Ca, Mg, S, B, Fe, and Cu disappeared, but not differences in Mn and Zn. Carbon dioxide enrichment of celery (*Apium graveolens* L.) decreased shoot levels of N, P, K, Mg, and B from 4 to 12% (Tremblay *et al.*, 1988). In roots, concentrations of N and K were reduced, Mg was increased (34%), and P, Ca, and B were unchanged. Nitrogen addition increased the N concentration of both roots and shoots, but caused reductions of P, K, and Ca levels in roots. Fertilization with P increased root and shoot P concentration, but lowered K in the shoot. In a study of three grass species (*Agrostis capillaris, Poa alpina* L., and *Festuca vivipara* L.), Baxter *et al.* (1994) reported that total nutrient absorption was greatest in *A. capillaris,* while N and K remained unchanged in *P. alpina*. In *A. capillaris* neither nutrient use efficiency (dry matter accumulated per unit of nutrient) nor nutrient productivity (dry weight gained per day over a defined period per mean weight of nutrient over the same period) was significantly affected by a doubling of CO_2. Depression of tissue nutrient content arose from increased growth instead of differences in nutrient use efficiency. The productivities of K, Mg, and Ca in *P. alpina* were lowered by elevated CO_2, while photosynthetic N and P use efficiencies were doubled. Poor growth of *F. vivipara* was accompanied by a decline in photosynthetic N use efficiency and photosynthetic P use efficiency and a large rise in the ratio of nonstructural carbohydrate to N content.

Plant tissue nutrient concentration is largely determined by plant roots, because these are the primary means of extracting nutrients from the soil profile. Therefore, effects of atmospheric CO_2 on roots, and belowground processes, will affect plant nutrition. Variability in the literature predicates that generalizations regarding the interacting effects of nutrients and CO_2, both in regard to growth and tissue nutrient content, be made with caution. In some cases, limited nutrient supply appears to inhibit only slightly plant growth response to CO_2 enrichment, and elevated CO_2 appears to aid plants in partially overcoming nutrient stress; in other experiments, positive growth responses to increased CO_2 are only observed when nutrients are not limiting. Nonetheless, it appears certain that critical nutrient concentrations will need to be reconsidered in light of the rising level of atmospheric CO_2. In addition, elevated CO_2 usually increases the overall size of plants, thus increasing whole-plant nutrient uptake for many plant species, but these nutrients are distributed throughout larger plants and, thus, concentration per unit weight of tissue is diminished. Also, nutrient utilization efficiency (unit of biomass produced per unit of nutrient) generally rises under elevated CO_2 (Gifford, 1992), while nutrient uptake efficiency (unit of nutrient per unit weight of root) declines in most studies. Plants under high CO_2 are able to produce more biomass with available nutrients; however, their larger root systems appear unable to gather proportionally more nutrients.

Nutrient supplies are critical to plant systems and attenuate the dynamic flows (Fig. 1) of essential materials (e.g., carbon and water) through them. Perhaps the principal difference between agricultural and natural ecosystems is that in the former, we seek, by whatever means that are economically feasible and environmentally sound, to minimize stresses on plant growth. Part of this "agri-culture" is to fertilize, to reduce nutrient stress. But in the wilderness meadow and backcountry forest, soil fertility is fixed. Here nutrients are in short supply and must be competed for, used sparingly and efficiently, and then recycled for yet another wave of hungry critters. The key role of nutrients in the changing global C cycle must be elucidated if we are to predict how these changes will impact ecosystem structure, function, and stability.

V. Soil Carbon Storage

Brinkman and Sombroek (1996), in discussing the reaction of soil conditions in relation to plant growth and food production in the context of global change, suggested that soil quality could be affected by changes in organic matter, soil biology, fertility, temperature, and hydrology; heightened soil resilience to degradation was also seen as a possible outcome. Increases in plant growth above and below the ground under increased atmospheric CO_2 have been well substantiated (Rogers and Dahlman, 1993; Rogers *et al.*, 1994; Goudriaan and Zadoks, 1995). Post *et al.* (1992) underscore the complexity of C fluxes as they dynamically interact with the global biogeochemical-climate system. They go on to say that it is "essential that we understand how terrestrial vegetation and ocean processes respond to changes in CO_2 and climate."

Woodward *et al.* (1991) have pointed out that the enormous propensity for CO_2 to stimulate plant growth has great potential for C sequestration in terrestrial ecosystems. However, Schlesinger (1986, 1990) found little evidence for soil C storage. Schlesinger (1995) further suggests that a lack of response of natural vegetation to higher CO_2 levels is likely to result from nutrient limitations.

Not only is soil fertility essential to terrestrial C sequestration, but as Tiessen *et al.* (1994) have argued for tropical soils, the recycling of nutrients from soil organic matter is necessary to maintain fertility (Fig. 1). Nepstad *et al.* (1994) have demonstrated the vital role of deep rooting in C deposition to soil in Amazonian forests. In these forests, there is more C below 1 m than above the ground. Pregitzer (1993) suggested the possibility that increased C flux to the soil may enhance available N and further noted that warmer temperatures could lead to faster decomposition and hence a more rapid return of CO_2 to the atmosphere. Pregitzer *et al.* (1995) also reported that production and mortality of fine roots, which can be the greatest source of C input to forest soils, were both increased under elevated CO_2 and as soil N availability increased. Nitrogen plays a key role in C storage in both plants and soils, and will therefore be pivotal in C processes affected by elevated CO_2 (Davidson, 1995).

Rastetter *et al.* (1992) used a general model of ecosystem biogeochemistry to examine C sequestration in two systems (arctic tundra and temperate hardwood forest). Increasing CO_2 increased C storage in both systems due to gains in C:N ratio in plants and soil. In a modeling study of soil organic C storage, Kirschbaum (1993) showed that equilibrium soil C content would increase with increasing rates of N addition (from atmospheric deposition and biological fixation). Hudson *et al.* (1994), employing a global C cycle model, have found that it is likely that a sizable part of the missing CO_2 sink is attributable to fertilization by N emitted from anthropogenic sources.

Huettl and Zoettl (1992), in discussing forest fertilization for enhanced C storage capacity, concluded that proper nutrient management may increase C in forest systems by stimulating biomass production both above and below the ground. Nilsson (1993), in fact, has observed an increase in C sequestration rate after fertilization of a Norway spruce [*Picea abies* (L.) H. Karst.] forest.

Leavitt *et al.* (1994), using $\delta^{13}C$ analysis of free-air CO_2-enriched cotton, observed that about 10% of the soil C had been replaced with "fresh" C, including the more recalcitrant fractions, in 3 yr of elevated CO_2 exposure. They suggest that the soils may be acting as an enhanced C sink under high CO_2. Follett (1993) states that, through improved management, agriculture (including forestry) has a great opportunity to help mitigate potential climate change by "stashing" CO_2 as C in soil and vegetation. He concludes that these practices can offset not only the CO_2 emissions from U.S. agriculture, but also part of that from U.S. sources outside of agriculture.

Stewart *et al.* (1992) have considered the interactive nature of global C and nutrient element cycles; they underscore the critical need for an integrated understanding if our actions to mitigate change are to be effective. For agricultural ecosystems, the management of crop residues is key to soil retention of C (Stewart, 1993).

VI. Conclusion

Predicting how belowground processes respond to rising CO_2 will be necessary for the management of future crop and forest systems. Among the most important of these processes is the absorption of mineral nutrients from the soil by roots. The following statements summarize what we know of the relationships of elevated CO_2 and plant nutrition:

- More CO_2 tends to result in positive responses in the belowground portion of plants and this has the potential to alter significantly the edaphic environment through increased carbon deposition and/or nutrient uptake by plants.
- Enhanced plant health and higher soil fertility levels through increased interactions with microbial symbionts under CO_2 enrichment appear likely.
- Rhizosphere and soil microbes may improve plant growth under CO_2 enrichment by increasing nutrient cycling and availability, and by improving soil quality through increased C storage.
- Critical nutrient concentrations (fertilizer recommendations for crops) will need to be reconsidered in light of the rising level of atmospheric CO_2.
- Elevated CO_2, through increased plant size, increases whole-plant nutrient uptake but concentration per unit weight of tissue is diminished.
- Plants under high CO_2 are able to produce more biomass with available nutrients, so nutrient utilization efficiency is generally increased.
- Larger plant root systems produced under elevated CO_2 appear unable to gather proportionally more nutrients, so nutrient uptake efficiency declines.
- Plant growth stimulation by CO_2 and higher C : N ratios suggest the potential for increased C sequestration in terrestrial ecosystems.

The relationship of carbon to factors such as mineral nutrition must be understood as we seek to mitigate and adapt to global environmental change. Knowledge of how plants and soils will respond to and sequester carbon is essential. We recognize the importance of carbon's edaphic interactions, and it is imperative that we develop a thorough understanding through further research.

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