1 Plant Responses to Atmospheric Carbon Dioxide Enrichment: Implications in Root–Soil–Microbe Interactions

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ABSTRACT

As CO_2 continues to increase in the global atmosphere, uncertainties associated with its effects continue to mount. There are indirect effects related to predicted climatic shifts and direct effects linked to its effect on plant metabolic processes and performance. Carbon dioxide is a major feedstock as well as a regulator of plant growth. As such it is essential to autotrophic plant life. The growth of the whole plant is often stimulated when CO_2 levels are increased. The development of leaves, stems, roots, and reproductive parts may be positively affected. The stimulation of root system development immediately leads to hypotheses of changes in rhizosphere microbiology and alterations in soil formative processes. Enhanced plant growth also suggests greater delivery of C to soil, and thus potentially greater soil C storage. Enough hard won data on the effects of elevated atmospheric CO_2 on the soil–root–microbe complex are available to show a clear linkage; however, the story is far from complete but early indications are that it will be an important one. Nonetheless, with an array of new techniques visible on the horizon, a solid understanding is sure to follow.

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Arguably the most important aspect of global change, the rise in atmospheric CO_2, is an undisputed fact. Emanating from our energy-rich lifestyle, elevated CO_2 levels will have far-reaching consequences for both physical and biological earth systems. Implications of the increase in atmospheric CO_2 concentration for the plant world have been previously reviewed (Krupa & Kickert, 1989; Wittwer, 1990; Allen, 1994; Rogers & Dahlman, 1994). A growing body of experimental evidence shows that effects of elevated CO_2 on plant life can be significant; however, because a good deal of the business of terrestrial vegetation occurs belowground, responses of roots, associated microbes, and soils must be understood if a full picture of CO_2 effects on vegetation is to be developed.

ENERGETICS

Photosynthesis

In the context of photosynthetic chemistry, there are three main plant groups, C_3, C_4, and CAM (Crassulacean acid metabolism). Three and four refer to the number of C atoms in the first molecules formed in the CO_2 fixation pathway. Soybean[1], wheat, rice, and potato are examples of C_3 plants. The C_4 pathway is found in tropical grass crops like corn, sugarcane, and sorghum, but is almost never found in woody species. Photosynthetic efficiency is greater in C_4 plants than the C_3s. In C_3 plants, 20 to 50% of the C fixed is immediately lost by photorespiration, while the C_4 plants exhibit little photorespiration. The remaining group, the CAM plants, are a form of C_4 except that CO_2 is fixed at night and then processed via a C_3 pathway during the day. The CAM plants include such species as pineapple and succulent vegetation like cacti and stonecrops; they are highly efficient in the use of water.

The photosynthetic machinery initiates the flow of energy in the metabolic reactions of the plant. Photoassimilates are converted to starch in the chloroplast for temporary energy storage or transported to sinks where they are used as sources of energy, converted to cellular constituents or converted to storage forms. The energy–generating process of dark respiration serves as a back–up system to the photosynthetic machinery in the leaves and is the source of energy generation in the roots and other non-chlorophyllous tissues (Kosuge & Kimpel, 1981). Consumption of C by dark respiration and photorespiration works in opposition to photoassimilation and detracts from yield.

The net amount of energy stored in the biosynthetic products of the plant determines its yield, which is the ultimate product of light energy capture and photoassimilation. Under normal circumstances a relatively small proportion of biosynthesis is directed to maintenance and replacement of cellular structures subjected to turnover. Maintenance respiration detracts <20% from the total amount of C assimilated by the plant because most of the intermediates released by turnover would be recycled into the main stream of the metabolism.

[1] Scientific names of plants mentioned in the text are given in an appendix at the end of the chapter.

In addition to the maintenance costs, plants must frequently expend additional energy for compensation or repair against various forms of biotic and abiotic stress. In the end, the observed biomass or yield is a product of: [(any stress effect) – (repair)] + [maintenance]. If stress effect exceeds repair costs (excluding normal maintenance costs), then there will be an adverse effect on biomass and/or yield. To the contrary, if repair costs exceed the stress effect, there will be no negative effect on biomass and/or yield. Elevated CO_2 concentrations essentially act as stimuli facilitating biosynthesis to exceed the normal maintenance and any stress repair costs, leading to higher plant biomass and/or yield.

High levels of CO_2 stimulate photosynthesis, particularly in C_3 plants. This is caused by the higher CO_2 *per se*, because both CO_2 and O_2 compete for the same site on the enzyme rubisco (ribulose-1,5-*bis*phosphate carboxylase; Goudriaan et al., 1990). The C_4 types are much less affected because photorespiration is already suppressed by a CO_2-concentrating mechanism (Poorter, 1993). The C_4 plants are quickly saturated as CO_2 concentration rises, while in the C_3 species photosynthetic responses continue to rise across a range extending more than several hundred μmol mol^{-1} CO_2. Limited data on CAM plants (their stomata close during the day) suggest that nocturnal enrichment of CO_2 would be beneficial (Black, 1986). Both increases in net photosynthesis and growth have been observed for CAM plants at elevated CO_2 concentration (Nobel & Hartsock, 1986). The overall subject of photosynthesis at elevated levels of CO_2 has been critically reviewed by Bowes (1991), Lawlor and Mitchell (1991), and Long and Drake (1992).

Despite the many studies showing stimulation of plant growth, the idea of photosynthetic acclimation leading to little or no long term gain in growth has been examined (Delucia et al., 1985; Peet et al., 1985; Sasek et al., 1985; Tissue & Oechel, 1987; Sage et al., 1989; Lawlor & Keys, 1993). The initial high level of photosynthesis that occurs when plants are first exposed to higher CO_2 levels may decline after a period of days or weeks. But, Drake (1992b) has pointed out that, even in the most extreme cases, photosynthetic rate falls only to that of control plants under ambient concentrations, and that these are unusual instances. Most investigations, however, even in those cases showing photosynthetic reductions, have demonstrated that rates of photosynthesis are sustained significantly above those expected under present day ambient CO_2 levels.

Source–Sink Relationships and Root Restriction

The crucial role of source–sink relationships in CO_2 growth response has been pointed out (Lawlor, 1991), and considerations of sink activity (i.e., C partitioning among the various plant organs) may help interpret divergent findings with regard to photosynthetic capacity (Herold, 1980; Cure et al., 1987, 1991; Drake, 1992b). Grodzinski (1992) points out that during CO_2 enrichment the source-to-sink balance within plants will change more rapidly than under ambient CO_2 levels.

Sionit et al. (1984), by comparing the response of container and field grown soybeans, concluded that stress imposed on plants by confining the roots may appreciably decrease the magnitude of their photosynthetic response to atmos-

pheric CO_2 enrichment. A literature survey by Arp (1991) revealed a strong correlation between pot size and photosynthetic capacity. Pot volume also influenced R/S (root/shoot ratio); it increased with lack of restriction but decreased with smaller pot size. For field-grown plants, either no reduction or an increase was seen in photosynthetic capacity with extra CO_2. The impact appeared to be related to the imbalance in source–sink relations brought about by the spatial restriction of root growth. Thomas and Strain (1991) have provided a detailed experimental investigation of photosynthetic acclimation of cotton seedlings to elevated CO_2 with root restriction as a main factor. They found that reduced photosynthetic capacity could be restored by simply repotting to larger containers, thus reducing root restriction. Progressive reduction of photosynthetic capacity as root growth space became smaller indicated a possible sink-limited feedback inhibition of net photosynthesis. Root system response to CO_2 immediately suggests changes in belowground competition and, thus, potential shifts in community structure and function. Root competition (McConnaughy & Bazzaz, 1991, 1992) and resource partitioning (Parrish & Bazzaz, 1976) may affect source–sink relationships. Other authors have considered this matter and have shown an array of effects of root restriction on aboveground plant physiology and morphology (Herold & McNeil, 1979; Carmi & Huer, 1981; Krizek et al., 1985; Tschaplinski & Blake, 1985; Hameed et al., 1987; Robbins & Pharr, 1988; Peterson et al., 1991a,b).

Coleman and Bazzaz (1992) aptly point out that root restriction may be a characteristic of some natural habitats so that unrestricted rooting volume may be as unrealistic as small pots. Also, some new evidence (McConnaughy et al., 1993a,b) shows that pot size may not affect plant CO_2 responsiveness. Berntson et al. (1993) measured over time root growth within pots to provide insight into the effects of CO_2 on the usage of belowground space by plants. They correctly state that plants in the field do not have unlimited belowground resources. It is interesting that in their study, pot shape influenced growth and reproduction. This may be related to changes in root architecture under elevated CO_2 (Rogers et al., 1994).

Root sensing of available soil water with subsequent direct signals that exert regulatory effects on shoot growth and functioning are being explored (Davies & Zhang, 1991), and these processes may well be involved in source–sink questions. Masle (1992a) considered the possible improvement of plant performance under atmospheric CO_2 enrichment on soils prone to dry conditions or with high mechanical impedance. While improvement of plant performance is probable, sink limitations induced by root signals need to be investigated to understand the role of elevated CO_2 in such situations (hard, dry edaphic conditions). Masle (1992b) further suggested that plant performance regulating signals also may be triggered by soil impedance to roots. Such direct communication could be pivotal to understanding aerial CO_2 effects on roots.

These studies point to a need to consider rooting volume in the design of CO_2 effects research. Not only is the work essential for a more complete understanding of CO_2 response, but also for developing a better picture of plant reaction to edaphic stresses.

Respiration

Although much research regarding the influence of CO_2 on growth and photosynthesis has been conducted, relatively little effort has been directed toward the influences of elevated CO_2 on plant respiration; however, enough studies have been conducted to suggest that changes in plant respiration may be important in the C dynamics of terrestrial ecosystems as the atmospheric concentration of CO_2 continues to rise (Wullschleger et al., 1994). Up to 50% of C fixed in C_3 plants may be lost due to respiration (Amthor, 1989; Farrar, 1985). Although few studies have attempted to determine the role of CO_2 in direct and indirect respiratory effects, CO_2 has been hypothesized to influence respiration in several ways. Higher levels of CO_2 tend to decrease specific leaf surface area (Ford & Thorne, 1967; Hurd, 1968; Clough & Peet, 1981; Garbutt et al., 1990), which may be indicative of thick cell walls and greater C content. This may increase the energy cost of constructing foliage per unit area. Although proteins have a high construction cost and increased protein content is associated with increased maintenance costs due to turnover, leaf protein and N content tend to decrease with increasing CO_2 (Cure et al., 1988). Therefore, total costs of tissue construction and maintenance may be decreased with elevated CO_2. Carbon dioxide increases in the atmosphere tend to increase root growth more than aboveground growth (Prior et al., 1994b; Wittwer, 1978). Because respiration of roots is significantly higher than aboveground portions per unit dry weight (Farrar, 1981), a tendency to increase respiration on a whole plant basis would result from elevated atmospheric CO_2. It also has been hypothesized that, because respiration rates of fungi are higher than for vascular plants, increased mycorrhizal colonization of plant roots under elevated CO_2 (Lamborg et al., 1983) may increase whole-plant respiration. Elevated CO_2 may result in greater activity of the cyanide resistant respiratory pathway that results in greater rates of respiration (Musgrave et al., 1986) and increase in nonstructural carbohydrates (Amthor, 1991). Because of this, another mechanism exists that could account for an effect of elevated CO_2 on plant respiratory costs. Although the biochemical bases for respiratory responses to ethylene are unclear, it is a strong promoter of respiration and CO_2 can influence ethylene biosynthesis (Amthor, 1991).

A reduction in dark respiration by elevated CO_2 has been found for several species. Both short-term and long-term responses have been reported. Gifford et al. (1985) demonstrated that high CO_2-induced suppression of dark respiration led to higher dry weight in wheat. Similar findings were reported for alfalfa by Reuveni and Gale (1985). Reuveni et al. (1993) reported suppression of respiration by high levels of CO_2 in plants representing several different physiological groups. Bunce (1990) observed inhibition of respiratory CO_2 efflux with increased CO_2 in two C_3 species, tomato and soybean, and in one C_4 species, amaranth. Reduced respiration has been seen in the field for three herbaceous perennial species, orchard grass, perennial rye grass, and alfalfa (Bunce & Caulfield, 1990). A doubling of CO_2 inhibited respiration of curly dock by 25 to 30%, while a decrease in CO_2 elicited a corresponding increase in respiration (Amthor et al., 1992); however, preliminary results from our work indicate that

resource limitations (i.e., N and water) had strong effects on the respiration of longleaf pine, but the effect of CO_2 was not significant. Implications of these phenomena for real-world plant systems will have to await further research. Such findings may call for a redesign of some present day experimental protocols (e.g., elevation of CO_2 both day and night).

Ryan (1991) suggests that data on respiration are difficult to interpret because construction and maintenance respiration were rarely distinguished and respiration was related only to dry weight or surface area and not to N content. In particular, separating effects on functional components of respiration (i.e., construction, maintenance, and ion uptake) as well as carbon costs due to root exudation is needed. These gaps in our knowledge hamper the development of adequate models that can assess the response of plant respiration to elevated CO_2 and represent major uncertainties concerning the effects of CO_2 enrichment on the C cycle.

ROOTS

In their 1918 bulletin, "The Aerial Fertilization of Plants with Carbon Dioxid", Cummings and Jones provide a report on the influence of CO_2 level on underground plant structures. Radish and potato were both positively affected by increased CO_2. Radish roots gained more biomass than stems. Growth was faster in the plants exposed to high CO_2; they were edible sooner and had more carbohydrates and less protein. For potatoes, tuber formation did not occur any sooner, but once started was faster, and better tubers were produced. Fifty years later, Tognoni et al. (1967) reported a general promotion of root growth by higher than prevalent atmospheric levels of CO_2 at that time, with accompanying increases in root/shoot ratios. They go on to state that in their experiments the most significant morphological effect of elevated CO_2 was the pronounced stimulation of root growth. They also suggest that the "beneficial effects of an increase in atmospheric CO_2 on the yield of root crops such as carrots or beets may be even more significant than on crops grown for their fruit, leaves, or stems."

Since then a number of investigations on plant responses to elevated CO_2 have included roots, but the consideration these vital plant organs have received has been minor and often cursory. Acock and Allen (1985) in their review of 184 research reports on crops found that, with the exception of a general increase in root to shoot ratio on a dry weight basis (R/S), there exists a serious lack of information regarding root growth response to elevated CO_2.

The paucity of data on belowground processes has been of concern to several investigators. Recently the results of more detailed studies on CO_2 enrichment and plant roots have begun to appear in the literature. Root growth and morphology as influenced by elevated CO_2 have been the object of several of these investigations. These types of studies are an excellent starting point, because the location and density of root components within the soil profile largely determine nutrient acquisition, especially for ions with low diffusivity, such as phosphate (Ikram, 1990; Caldwell et al., 1992).

Stulen and den Hertog (1993) have provided a critical review of the available literature concerning the effects of elevated atmospheric CO_2 on plant root

growth and function. They discuss several experimental parameters that influence the response of roots to CO_2 (e.g., water, nutrients, and pot size) and state that much of the variability in responses (particularly in regard to root/shoot ratio) seen in the literature can be attributed to differential treatment of plants during experiments. They conclude that more research on belowground plant growth and function is required, and that CO_2-induced changes in dry matter allocation to roots needs to be critically reconsidered.

We have recently completed a review of 167 studies on root response to elevated CO_2 concentrations (Rogers et al., 1994). The most frequently examined root response to elevated CO_2 has been dry weight, in approximately half of the studies. Root dry weight increased under elevated atmospheric CO_2 in about 87% of the studies regardless of species or study conditions. Roots often exhibited the greatest relative dry weight increase among plant organs under high CO_2 (Wittwer, 1978; Rogers et al., 1983; Imai et al., 1985; Norby et al., 1992). Similarly, an increase in biomass partitioning to roots (expressed as an increase in the percent dry matter in roots) was sometimes observed (Imai & Murata, 1976; Hocking & Meyer, 1991; Ziska & Teramura, 1992). Results on R/S have been highly variable; increases in R/S were found in about 41% of the studies examining this response variable. Newton (1991), in summarizing findings from 10 studies, reported that R/S increased in nine species, decreased in four, and showed no change in three; this variable pattern of R/S response to elevated CO_2 was approximately the same for groups of C_3 and C_4 plant species. In another investigation of 27 herbaceous species, results of R/S response to elevated CO_2 were mixed; R/S decreased in 14 species; increased in six; and seven species showed no response (Hunt et al., 1991). Ryle and Powell (1992), studying the influence of elevated CO_2 on defoliation of white clover under controlled conditions, found that biomass yield increased by 45% and, while root growth did not increase, R/S decreased; this is to be expected with defoliation stress. Chu et al. (1992) found that root-shoot partitioning in wild radish was unaffected by high CO_2 concentration but was correlated with daily starch accumulation.

A majority (77%) of the studies in our survey (Rogers et al., 1994) found that increased CO_2 resulted in more and/or longer plant roots that could possibly lead to their increased penetration of the soil profile (Baker et al., 1990; Rogers et al., 1992a) and/or spread (Idso & Kimball, 1991, 1992). Significant enhancement of root formation on plant cuttings has been observed with CO_2 enrichment (Grant et al., 1992). Improved rooting probably arose as a result of enhanced water relations rather than increased carbohydrate levels. Increasing the concentration of CO_2 in greenhouse mist systems increased the percentage of plant cuttings that form roots in numerous ornamental and floricultural species (Lin & Molnar, 1981; French, 1989). Elevated CO_2 during propagation also increased root number and length in sweet potato slips (Bhattacharya et al., 1985). Davis and Potter (1983) reported significant increases in root length and dry weight for several ornamental species, but found increases in root number only for peperomia. In a further study with leafy pea cuttings, elevated CO_2 increased carbohydrates, water potential, and root system size but not root number (Davis & Potter, 1989). In a field study of elevated CO_2 effects on a Chesapeake Bay wetland, Drake (1992a) noted increased numbers of roots and rhizomes (with increased

allocation of C to them) for the C_3 sedge, American bulrush. Doubled CO_2 doubled corm yield and roots of the C_3 tropical konjak (Imai & Coleman, 1983). In their review, Porter and Grodzinski (1985) reported a mean yield ratio of 1.40 for mature and 1.77 for immature root crops under CO_2 enrichment compared with the controls.

Del Castillo et al. (1989) tested the assumption that the extra root weight of high CO_2-grown soybean plants would enable them to explore a greater volume of soil. They found that root weight was 26 to 31% higher in CO_2 enriched chambers and that cumulative root length showed corresponding increases but CO_2 treatment did not affect the rate of root elongation. Instead, they found a significant linear increase in the number of actively growing roots with increased CO_2, i.e., the root systems of soybean plants growing under CO_2 enrichment were more branched than those growing in ambient air. They concluded that roots of soybean plants growing in high concentrations of CO_2 would not explore a greater volume of soil but would explore a given volume of soil more thoroughly. These findings are in contrast with those of Rogers et al. (1992a) who observed a 110% increase in root length of soybean plants under high CO_2, with no change in the number of lateral roots (Fig. 1–1). Also, Berntson and Woodward (1992) observed changes in both the architecture and development of root systems of common groundsel exposed to elevated CO_2 and water stress.

Chaudhuri et al. (1990) found that winter wheat grown under elevated CO_2 achieved maximum rooting penetration significantly faster than plants grown in ambient air. They also found that differences in root growth between ambient and elevated CO_2-grown plants occurred in the first 10 cm of soil depth and concluded that high levels of CO_2 can compensate for restriction in growth of wheat roots by drought, particularly in the upper 10 cm of soil. In contrast, Chaudhuri et al. (1986) found that numbers and dry weights of sorghum roots were higher at all soil depths (to 150 cm) under elevated CO_2.

Masle et al. (1990) developed a theoretical framework of the growth and C economy of wheat seedlings as affected by soil resistance to penetration and ambient CO_2 concentration. They found that high soil resistance appeared to induce a factor that reduced shoot growth, reducing its sensitivity to carbohydrate substrates and thereby making more C available for the roots; however, they further report that, as seed reserves become limiting, growth becomes sensitive to the level of atmospheric CO_2 and that this response to CO_2 was seen mainly in the roots, indicating that root growth appeared to be suffering from a C limitation under ambient CO_2. They concluded that, if atmospheric CO_2 were not limiting, the adaptive advantage of allocating more C to the roots would increase the chance for plants to overcome or recover from the difficulty of developing an inadequate rhizosphere in a soil of high mechanical resistance.

Laforge et al. (1991) found that raspberry plantlets rooted better under high levels of CO_2. They demonstrated that R/S increased 90% and that resource allocation to the root systems, measured as percentage of dry weight in roots, increased 75%; however, the largest increases were in root dry weight (189%) and in root number (220%).

Rogers et al. (1992a) demonstrated significant increases in root dry weight, volume, diameter (both stele and cortex), R/S weight ratio, as well as root length

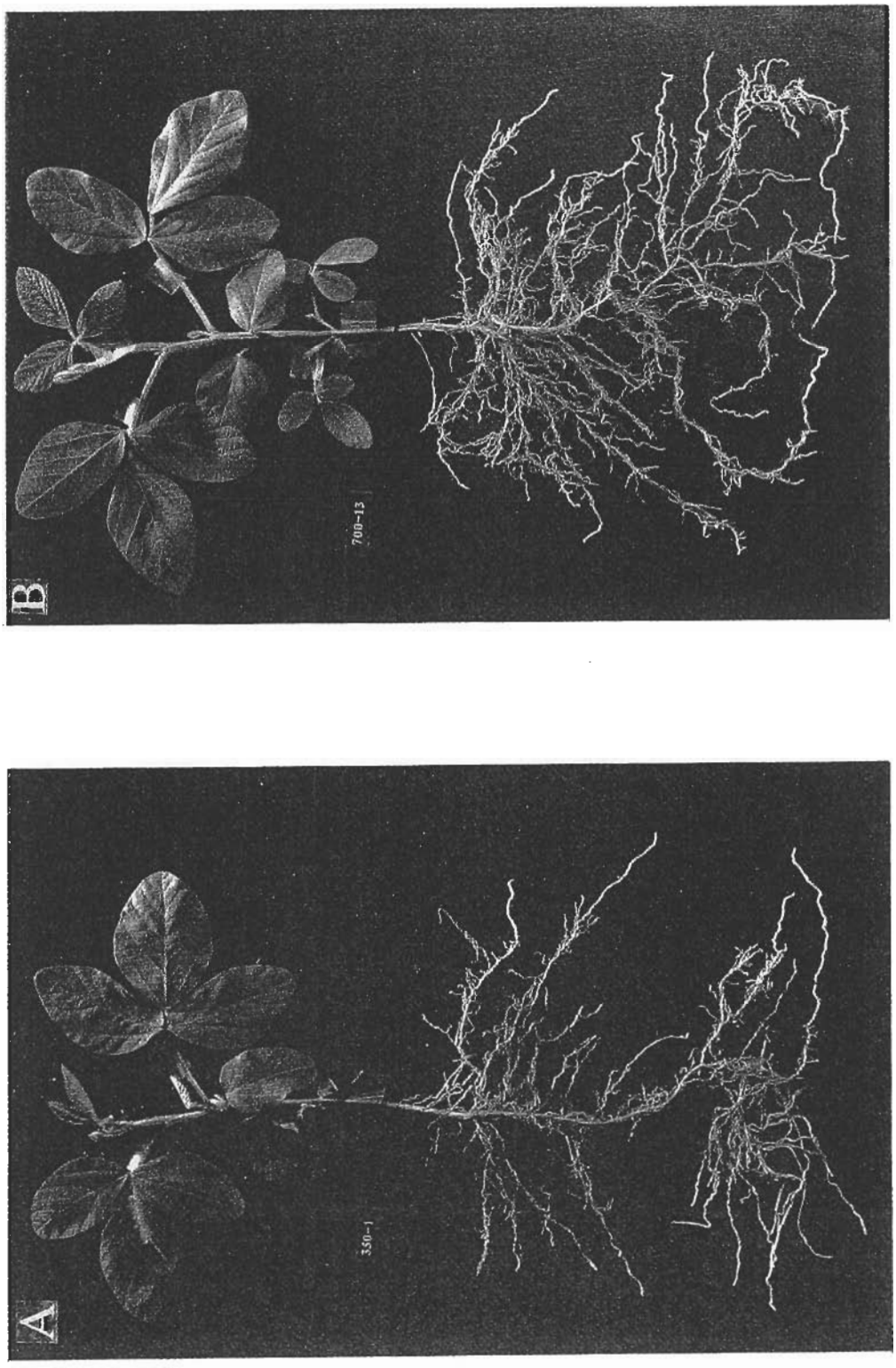

Fig. 1–1. Photographs of 18-d-old soybean plants grown at (a) 350 μmol mol^{-1} and (b) 700 μmol mol^{-1} CO_2. Photographs show the median plant, based on root length, for each treatment (Rogers et al., 1992a).

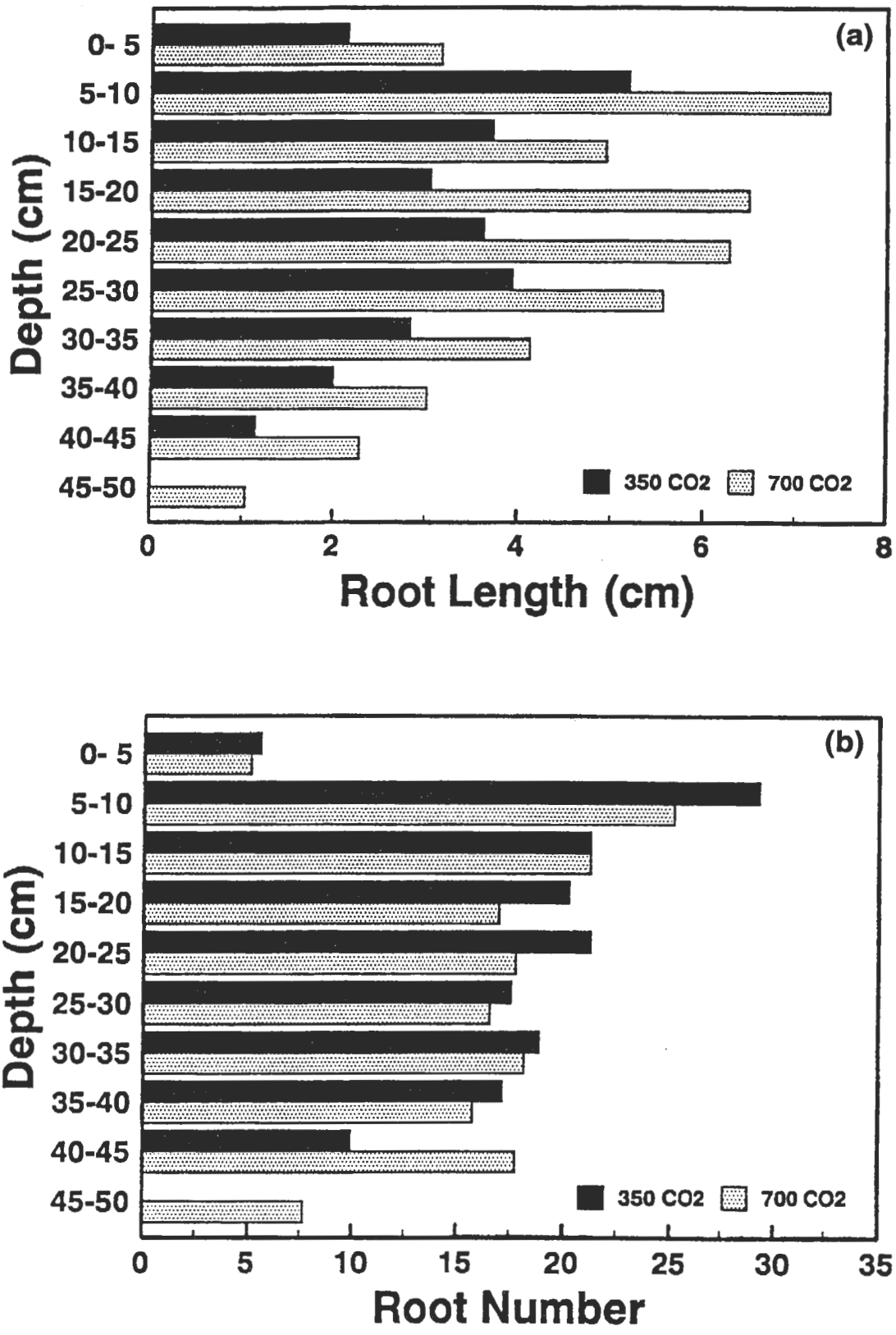

Fig. 1–2. (a) Length of first-order lateral roots with depth (n = 12) and (b) number of roots for the same 12 soybean plants with depth at 350 and 700 μmol mol^{-1} CO_2 (Rogers et al., 1992a).

at most soil depths to 50 cm, for high CO_2-grown soybean plants. Unlike length, neither total number of roots nor numbers of roots at specific depths exhibited response to CO_2 enrichment (Fig. 1–2).

Studies also have been conducted on belowground responses of cotton plants under Free-Air CO_2 Enrichment (FACE; Prior et al., 1994a,b; Rogers et al., 1992b). Dry weights, lengths and volumes of taproots, lateral roots, and fine roots were often significantly higher for CO_2 enriched plants. Although the numbers of lateral roots per unit length of taproot tended not to be significantly increased by elevated CO_2, the overall greater taproot lengths under CO_2 enrichment usually provided increased total numbers of laterals. A unique feature of this FACE cotton root research was the investigation of root architecture, i.e., the distribution of fine root density per unit volume of soil (expressed as length or dry weight per m^3) both vertically and horizontally (Prior et al., 1994a). The density of fine roots increased under CO_2 enrichment at most depths to 90 cm, but the increase was more significant in the upper 45 cm of the soil profile (Fig. 1–3). The root length and dry weight densities also tended to exhibit greater differences between ambient and elevated CO_2 treatments as horizontal distance from row center increased, indicating faster and/or more prolific spread of cotton roots through the soil profile under elevated CO_2 (Prior et al., 1994a). We are currently conducting similar studies on the effects of elevated CO_2 on soybean (C_3) and sorghum (C_4). Preliminary results indicate that, while CO_2 enrichment significantly increased biomass of all plant parts (with the exception of sorghum grain), the largest increase for both plants occurred belowground, i.e., root biomass increased 54 and 73%, for soybean and sorghum, respectively.

Substantial CO_2 research with some emphasis on the belowground component has been conducted at Oak Ridge National Laboratory, Oak Ridge, TN, with several forest tree species, including shortleaf pine (Norby et al., 1987; O'Neill et al., 1987b), Virginia pine (Luxmoore et al., 1986), white oak (Norby & O'Neill, 1989; Norby et al., 1986a,b; O'Neill et al., 1987b), yellow poplar (Norby et al., 1992; O'Neill et al., 1987a), and woody plants with N_2 fixing systems (Norby, 1987). Generally, all these tree species have shown increases in root dry weight, R/S, nutrient uptake, C allocation to roots, root exudation, and mycorrhizal colonization under elevated CO_2. Other detailed work conducted with two species of ornamental trees, Atlas cedar and Austrian pine, demonstrated positive but varying root responses to CO_2 enrichment, related by the authors to differences in phenological root growth patterns between the two species (Kaushal et al., 1989).

Research with species in a natural plant community has demonstrated increased root dry mass for American bulrush (C_3), but not for salt meadow cordgrass (C_4), at depths up to 15 cm, while roots of mixed communities of the two species were significantly different only at the 10- to 15-cm depth (Curtis et al., 1990). American bulrush, whether alone or in mixed communities, also showed lower percentage of N and, thus, higher C/N ratios when grown under elevated CO_2. Recent detailed studies in a tallgrass prairie ecosystem (Owensby et al., 1993b) have demonstrated increased root biomass production for some species that may have led, at least in part, to alterations in species composition. Other work in this ecosystem (Owensby et al., 1993a) with nutrient dynamics demon-

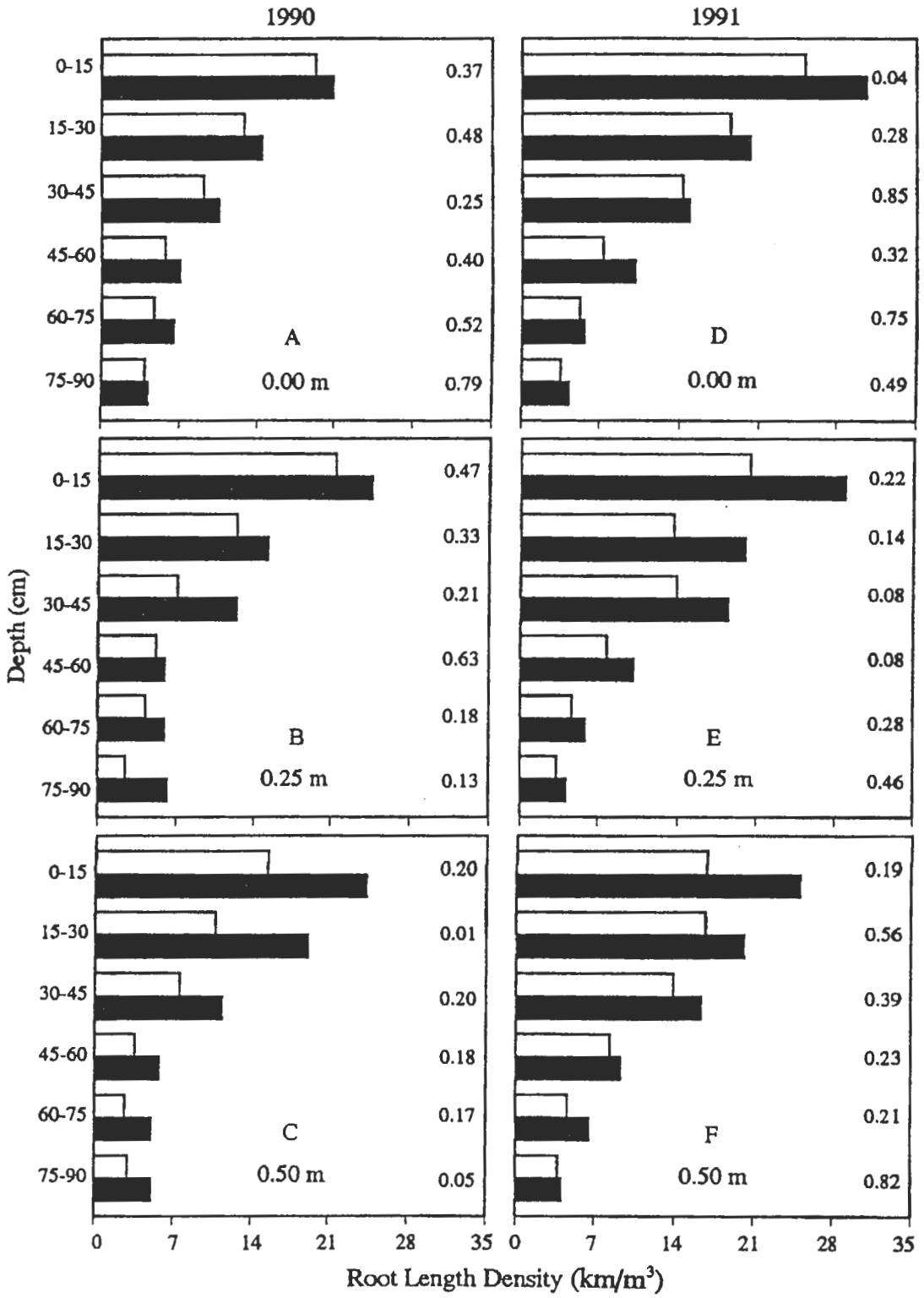

Fig. 1–3. The effect of CO_2 concentration (□ = 360 μmol mol^{-1}; ■ = 550 μmol mol^{-1}) on cotton root length density at various depth increments and positions (0, 0.25, and 0.50 m) away from the crop row during vegetative growth in 1990 (A, B, and C) and 1991 (D, E, and F). Means and probabilities are shown.

strated that total and/or root N and P contents tended to increase, while concentrations per unit dry weight of tissue tended to be lower under CO_2 enrichment.

Studies on such structural aspects of roots as 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 have been demonstrated to benefit from elevated CO_2 in most cases. Other response variables which increase under elevated atmospheric CO_2 include parenchyma cell division and expansion, carbohydrate concentrations in roots or tubers, and mycorrhizae (Rogers et al., 1994).

Distinct shifts in resource allocation patterns have been observed under elevated CO_2 conditions (Fajer et al., 1991; Coleman & Bazzaz, 1992). Luo et al. (1994) have provided an excellent framework for predicting response of photosynthesis and root fraction to elevated CO_2. The interactive roles of C, N, and growth were considered. The authors conclude that the response of root fraction tends to rise or fall if photosynthesis per unit leaf mass is more sensitive to changes in CO_2 concentration than relative growth rate. Hilbert and Reynolds (1991) have developed a model allocating plant growth among leaf protein, shoot structure, and root biomass to produce balanced activity. In addition to light and soil N, the model accounts for CO_2. Prediction by this model with respect to R/S ratios and leaf N concentrations in response to resource availability were consistent with experimental trends that are generally observed. Imai et al. (1984) observed a large increase in growth (150%) for the tropical root crop cassava, with a greater partitioning to the root fraction. Miao et al. (1992) noted a greater allocation to roots in elevated CO_2 treatments where a very dry soil water regime was used, suggesting more access to limited water supply.

Recently we reexamined the data previously collected by Rogers et al. (1983) on the dry matter partitioning in soybean (C_3) and corn (C_4) exposed for 11 wk to elevated CO_2 concentrations. Figures 1–4 and 1–5 show our results expressed as the ratios of the percentage of increase in the dry weight of various plant organs at three levels of elevated CO_2, in comparison to plants grown in 340 μmol mol^{-1} CO_2. The root (R) to total shoot (TS) ratio increased at all three elevated CO_2 concentrations in both plant species; however, the magnitude of such increase exhibited a curvilinear relationship in both cases, with the amount of increase declining from 520 to 718 μmol mol^{-1} and then, increasing again at 910 μmol mol^{-1} CO_2. An opposite pattern was observed with the stem (S) to leaf (L) ratios in both plant species. In comparison to these observations, while in soybean the R/S ratio exhibited a curvilinear relationship, in corn there was a progressive decline in these ratios with increasing CO_2 concentrations. As the CO_2 levels increased from 340 μmol mol^{-1}, progressively more dry matter was allocated to the stems, in comparison to the roots. While such differences in carbon allocation and dry matter partitioning between C_3 and C_4 plants may not be surprising, we are unable to explain the curvilinear relationship between the ratios of percentage of increase in the dry matter of various plant organs and changing CO_2 concentrations. Although our studies may represent the only example at the present time, the observed inflection point at ~700 μmol mol^{-1} CO_2 (Fig. 1–4 and 1–5) may be of great interest and requires confirmation and further investigation. The overall observations may have a role in differentially regulating the architecture of C_3 vs.

C_4 plants at different levels of elevated CO_2 and, thus, leading to possibly differing outcomes in crop-weed competitions at different CO_2 levels when C_3 and C_4 plants are involved.

RHIZOSPHERE

The rhizosphere is the narrow zone of soil around plant roots in which soil microbial activity is affected by the root and rhizodeposition into the soil (Curl & Truelove, 1986). Rhizodeposition is the release of organic materials from plant roots into the rhizosphere. These materials include: exudates such as sugars, amino acids, organic acids, and enzymes; sloughed roots, root hairs, and root cells (especially from the root cap); mucilages from the plant and microorganisms; and other compounds (Curl & Truelove, 1986; Campbell & Greaves, 1990). Rhizodeposition has been quantified through the exposure of plants to $^{14}CO_2$ and published values vary between 2 and 30% of C assimilated by photosynthesis (Whipps, 1987; van Veen et al., 1989). Such rhizodeposition is intimately linked

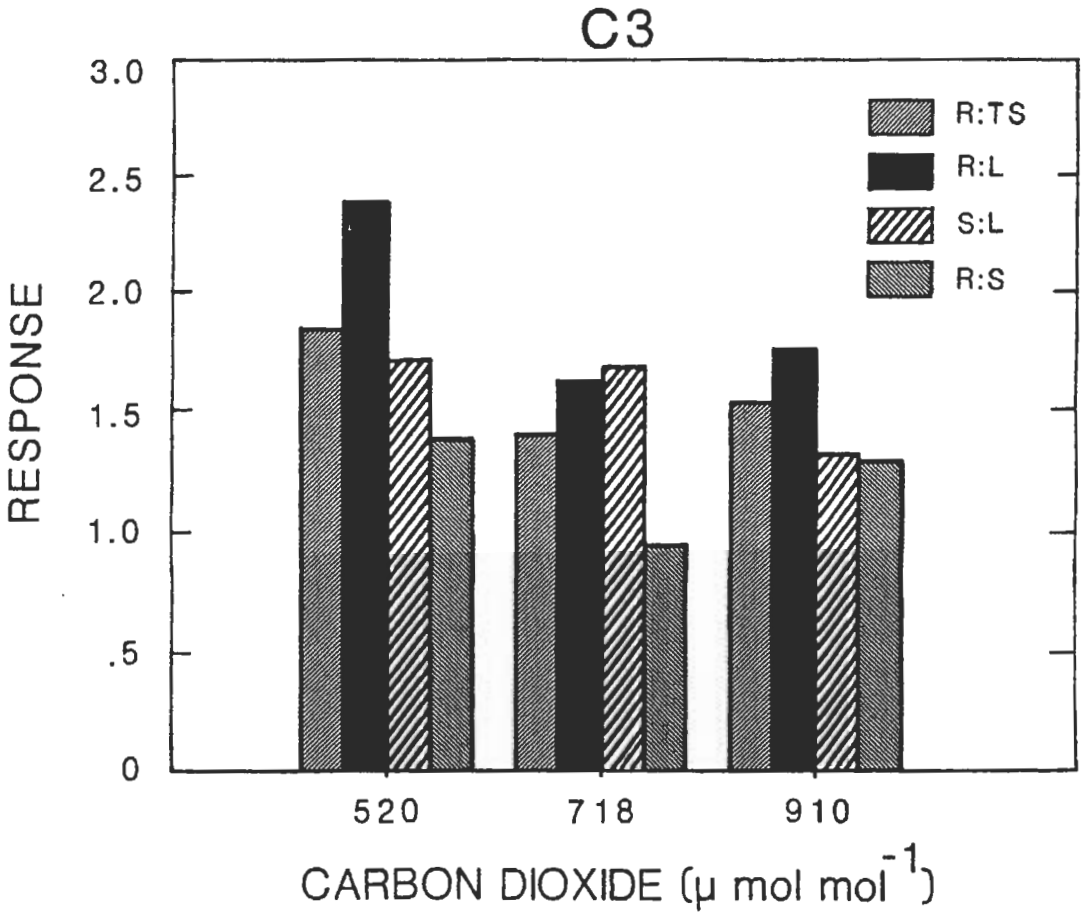

Fig. 1–4. Ratios of percentage of increase in dry matter partitioning to leaves (L), stems (S), roots (R), and total shoot (TS) in the C_3 species soybean (11-wk old) grown in open-top chambers at Raleigh, NC; CO_2 concentrations were 340, 520, 718, and 910 μmol mol^{-1}. Partitioning data were recalculated as a percentage of the dry weight of vegetative parts at 340 μmol mol^{-1} at each elevated CO_2 level (Rogers et al., 1994).

with rhizosphere microorganisms. The quantity and quality of rhizodeposition affect rhizosphere microbial composition and activity, e.g., rates of organic matter decomposition (Parkinson, 1988), and rhizosphere microbes can increase losses of materials from roots by up to 100% (Barber & Martin, 1976), which can, in turn, increase mobilization and acquisition of mineral nutrients (Marschner et al., 1990). The plant root, its rhizodeposits, and rhizosphere microflora and microfauna all interact to affect the overall health of the plant.

Certain microorganisms in the rhizosphere can benefit plant health by forming symbiotic relationships with roots. Examples include N fixing bacteria and actinomycetes, ecto- and endomycorrhizal fungi and plant growth promoting rhizobacteria. In addition to N_2 fixation and growth promotion in the specific systems, other benefits to the plant in the appropriate cases include, increased availability of water and nutrients, tolerance to adverse soil conditions such as low or high temperatures and high salt concentrations and protection against root pathogens (Marx & Krupa, 1978). In as much as plants derive benefits from these relationships, so do the associated microbes. The roots provide a C rich substrate for the sustenance of the microbial symbiont. Pang and Paul (1980) found that in

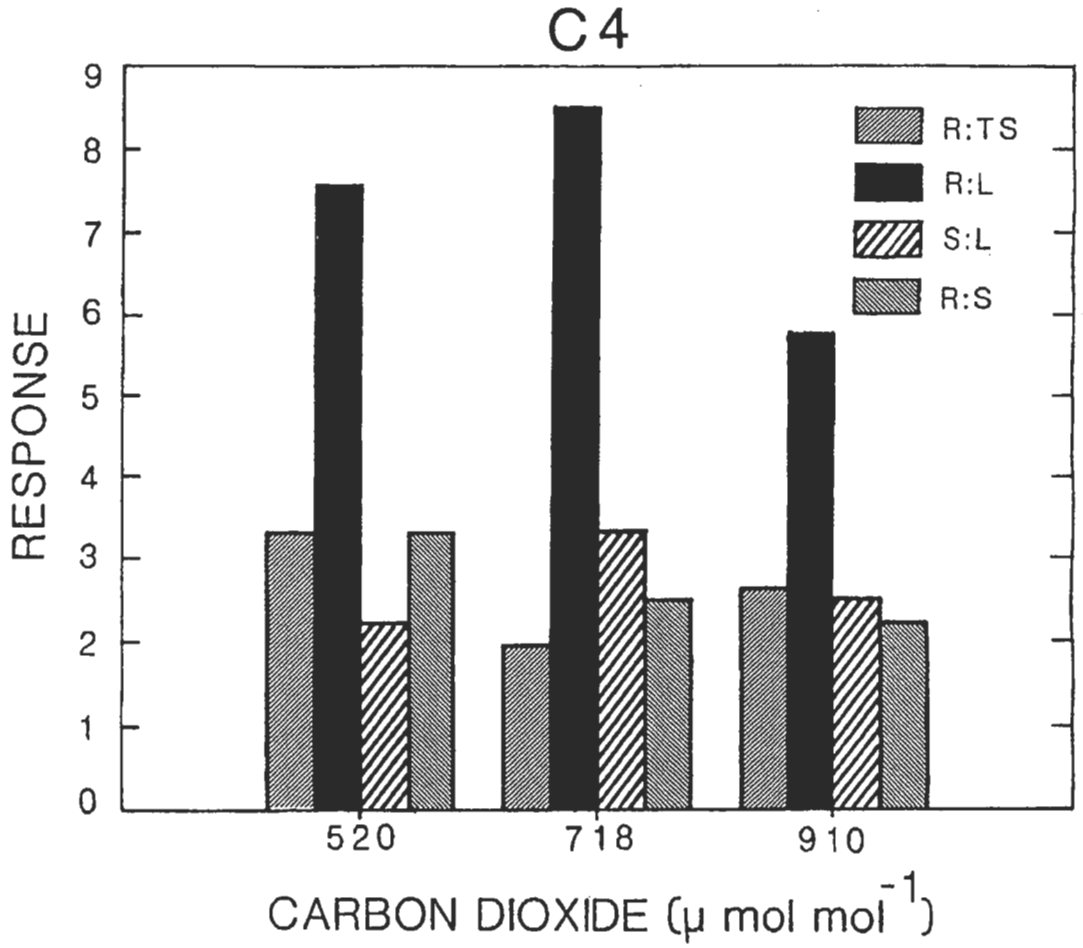

Fig. 1–5. Ratios of percentage of increase in dry matter partitioning to leaves (L), stems (S), roots (R), and total shoot (TS) in the C_4 species corn (11-wk old) grown in open-top chambers at Raleigh, NC; CO_2 concentrations were 340, 520, 718, and 910 μmol mol^{-1}. Partitioning data were recalculated as a percentage of the dry weight of vegetative parts at 340 μmol mol^{-1} at each elevated CO_2 level (Rogers et al., 1994).

comparison to nonmycorrhizal roots, additional C, equivalent to about 10% of the photosynthate, was allocated to the mycorrhizal roots of broad bean. Similarly, Kucey and Paul (1982) observed that N_2-fixing *Rhizobium* nodules of mycorrhizal broad bean plants used 12% of total photosynthate, whereas those of nonmycorrhizal plants only used 6%. The C-fixation rate also was increased by 8% in plants supporting mycorrhizal symbionts. Snellgrove et al. (1982) also found that leek plants translocated 7% more C to mycorrhizal compared with nonmycorrhizal roots of similar sized plants. The increased C allocation was associated with a decrease in specific leaf mass and increased leaf hydration. The authors suggested that this adaptation could enable mycorrhizal plants to maintain a greater photosynthetic capacity without increasing plant C requirements. According to Reid et al. (1983) mycorrhizal plants assimilated more CO_2, allocated a greater proportion to their root systems, and lost a greater percentage of radioactively labeled C by root respiration than nonmycorrhizal plants. These few examples show possible alterations in plant C balance induced by root–soil microbe interactions. We are only beginning to understand how these processes will be further modified by an enriched CO_2 atmosphere (this is discussed in a latter section of this manuscript).

In addition to the obvious benefits provided to plants from associations with symbiotic microorganisms, rhizosphere microorganisms are intimately involved in nutrient cycling. Microbes are responsible for the decomposition of organic matter and it is through the processes of decomposition and mineralization that nutrients become available to plants (Grant & Long, 1981). 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 concentration of nutrients that are mineralized by microbes and made available for plant growth (Grove et al., 1988). For example, microbial transformations of organic phosphorus often produce the majority of the plant available solution P (Paul & Voroney, 1980). Not only can soil and rhizosphere microbes make nutrients available to plants, they also can make them unavailable through immobilization. In an experiment with labeled ryegrass residues, Jenkinson (1966) found that 31 to 39% of labeled C remaining in the soil after 1 yr was present as microbial biomass. Soil microfauna also are extremely important in the nutrient mineralization/immobilization process. Microarthropods (Rabatin & Stinner, 1988) and nematodes (Ingham, 1988) are known to feed on hyphae of mycorrhizal fungi and, under heavy grazing, sufficient hyphae may be destroyed to detrimentally limit P uptake; however, nematodes and microarthropods that feed on rhizosphere bacteria and fungi can increase rates of decomposition, mineralization, and nutrient turnover by keeping the decomposing/mineralizing microbial populations in a more rapid phase of reproductive growth (Coleman et al., 1984; Freckman, 1988). Soil microfauna also can lead to increased nutrient availability to plants by reducing the amounts immobilized within microbial biomass (Freckman, 1988).

Root pathogens (which primarily include fungi, bacteria, and nematodes) represent another important component of the rhizosphere microflora. In addition to the obvious effects of pathogenic microbes on plant health (i.e., mortality, and reduced growth and yield), problems associated with the presence of such

microbes can lead to increased use of pesticides in agronomic or agroforestry ecosystems and can alter the composition and function of natural ecosystems (Shaw & Kile, 1991).

The rhizosphere, and its complex interactions with beneficial and detrimental microorganisms, will undoubtedly be affected by increasing levels of atmospheric CO_2. This influence of elevated atmospheric CO_2 is not likely to be direct because the concentration of CO_2 in the soil is already 10 to 50 times that existing in the atmosphere (Lamborg et al., 1983); however, plant mediated responses to elevated atmospheric CO_2 have the potential to alter rhizosphere microbial composition and activity, primarily by altering rhizodeposition. There are several excellent reviews on rhizodeposition and the rhizosphere (Newman, 1985; Whipps & Lynch, 1985; Curl & Truelove, 1986; Vancura, 1988; Whipps, 1990); however, relatively little is known concerning the effects of elevated atmospheric CO_2 on rhizodeposition. Van Veen et al. (1991) pointed to the paucity of data concerning the effects of CO_2 on C fluxes in plant–soil systems and speculated that increased plant biomass production under high CO_2 may lead to increased C inputs and increased microbial activity in the rhizosphere. Although Whipps (1985) found that the percentage of root-translocated C released from maize was not significantly affected by CO_2 concentration, Norby et al. (1987) observed that root exudation of soluble, ^{14}C-labeled compounds from shortleaf pine seedlings was greater in plants grown in CO_2-enriched air for up to 34 wk. Lekkerkerk et al. (1990) reported increases in C transported to all parts of the plant–soil system, including C lost through root exudation and soil/root respiration, proportional to the increase in photosynthetic fixation of C by plants at higher CO_2 levels. They also report that significantly more $^{14}CO_2$ was respired and a lower percentage of ^{14}C was retained in the roots of plants under elevated CO_2 when examined as a percentage of the amount of ^{14}C being translocated to the roots. Finally, Zak et al. (1993) found after 152 d significantly larger pools of labile C in the rhizosphere of plants grown in elevated CO_2; labile C in bulk soil showed no such change. Effects of elevated CO_2 on rhizodeposition may have important implications to the development of rhizosphere biota (Curl & Harper, 1990) including root disease suppression (Curl, 1988); however, little attention has been paid to this aspect of plant health.

Influences of atmospheric CO_2 on plants (C input and C/N ratio) and on soil microbes (composition and activity) also will affect C turnover and storage in soils. Lamborg et al. (1983) speculated that increased C input from increased biomass would lead to increased decomposition of organic matter and, thus, elevated atmospheric CO_2 would not result in accumulation of C in soil. Alternatively, Goudriaan and de Ruiter (1983) proposed that, due to preference of soil microbes for easily decomposable root-derived materials (rhizodeposition), increased level of CO_2 would retard decomposition of native soil organic matter and result in an accumulation of soil C. The debate remains unresolved, but studies are beginning to address this important issue. Melillo (1983) reported higher C/N ratios and higher levels of phenolic in sweetgum leaves exposed to high CO_2 and hypothesized that this would result in reduced rates of decomposition and decreased soil fertility. Ball (1992) found increased growth of a lignocellulose-degrading actinomycete on, and increased degradation of, ambient-grown wheat material, and

related this to increased lignification and/or changes in the C/N ratio of elevated CO_2-grown material. Lekkerkerk et al. (1990) found that input of easily decomposable root-derived material in the soil of 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 CO_2-enriched material, while the rate for control materials declined. These shifts in decomposer composition led to an overall enhancement of C mineralization by 30% for CO_2-enriched material. An increase in C turnover also was observed in soils that had supported CO_2-enriched cotton plants for three seasons (Wood et al., 1994) and this could be related to increases in soil microfauna and saprophagous nematode populations (Runion et al., 1994a).

The effects of increased atmospheric CO_2 on N fixation have been examined in several plant species. Legume/bacterial symbiosis is significantly increased by elevated CO_2 levels (Reddy et al., 1989; Reardon et al., 1990). Acock (1990) concluded that, in general, the increase in N fixation appears to be due mainly to larger biomass, i.e., bigger plants provide more C allocation for N fixation, and this is supported by the fact that some studies have found increased nodule dry weight under high CO_2 with no effect of CO_2 on specific (g N g^{-1} nodule) nodule activity (Finn & Brun, 1982; Williams et al., 1981); however, others have found significant increases in N_2 fixation under atmospheric CO_2 enrichment (Hardy & Havelka, 1973; Whiting et al., 1986) and related this increased activity to elevated CO_2 induced stimulation of photosynthesis. These differing results may be due to differences in plant species (Masuda et al., 1989a,b), experimental conditions, and duration and level of CO_2 exposure. Phillips et al. (1976) obtained results indicating that long-term enrichment promoted N_2 fixation by enhancing nodule development in peas while short-term high CO_2 exposures increased N_2 fixation by affecting nodule function. Other researchers have found increases in nodule development (i.e., increased nodule dry weight and increased nodule number per plant) and/or nodule function (i.e., increased nitrogenase activity, increased N_2 fixation, and increased whole plant N) under elevated CO_2 and these data have recently been summarized by Rogers et al. (1994). Also, studies have recently been initiated to examine the direct effects of increased levels of atmospheric CO_2 on the microbial symbionts (*Rhizobium* sp. or *Frankia* sp.) responsible for N_2 fixation (Ortega et al., 1992; S.R. Shafer, 1993, personal communication).

It has been hypothesized that elevated atmospheric CO_2 will result in increased colonization of plant roots by mycorrhizal fungi (Lamborg et al., 1983; Luxmoore, 1981), which in turn will promote plant productivity. The fact that mycorrhizal fungi can provide additional water to plants through hyphal proliferation in soil (Luxmoore, 1981) may, at least in part, explain the observed increase in biomass of CO_2-enriched plants under drought stress. Carbon dioxide enrichment increased colonization of roots of shortleaf pine (Norby et al., 1987; O'Neill

et al., 1987b), white oak (O'Neill et al., 1987b), and blue grama (Monz et al., 1992) by mycorrhizal fungi. Lewis et al. (1992) found that colonization by mycorrhizal fungi of loblolly pine seedlings from different geographic sources were differentially affected by CO_2 enrichment. Runion et al. (1994a) observed a trend for increased fungal colonization of cotton roots under FACE and reported that high CO_2-grown plants would have more mycorrhizae on a whole-plant basis due to their significantly larger root systems. In a recent report, Runion et al. (1994b) found that longleaf pine seedlings exposed to a twice ambient concentration of CO_2 had greater total numbers of ectomycorrhizae and a higher percentage of mycorrhizal short roots. They further reported that, due to increases in total fine root length and in mycorrhizal colonization, elevated CO_2 resulted in a doubling of the number of ectomycorrhizae per longleaf pine seedling. Overall increases in the development of mycorrhizae also may be due to the availability of higher concentrations of soluble C in the root system under atmospheric CO_2 enrichment and consequent stimulation of fungal infection and growth. In comparison, no reports to date have examined the effects of elevated atmospheric CO_2 on associations between plants and growth-promoting rhizobacteria.

Effects of CO_2 on rhizodeposition will drive changes in root–soil microbial composition and activity that will affect not only N-fixing bacteria and mycorrhizal fungi but also pathogenic and nutrient cycling microbes. Changes in the concentration of CO_2 in the soil *per se* are known to affect soil microorganisms (Gardner & Hendrix, 1973; Ioannou et al., 1977). Although data are beginning to be collected on effects of atmospheric CO_2 on aboveground pathosystems (Thompson, 1990), information on the effects of elevated atmospheric CO_2 on soil-borne pathogens and on root diseases are virtually nonexistent. Freckman et al. (1991) found no effect on nematode numbers or species composition when exposing cores of prairie soil to elevated atmospheric CO_2; however, Runion et al. (1994a) observed a trend toward decreasing numbers of parasitic nematodes in root-zone soil of cotton plants grown under high CO_2. These authors also reported a trend for increased populations of *Rhizoctonia solani*, a cotton root rot pathogen, but observed no corresponding increase in root disease in a bioassay using root-zone soil from high CO_2 grown plants. The manner in which increases in atmospheric CO_2 will affect plant diseases is of vital importance to managed and unmanaged ecosystems and deserves increased attention.

Microbes are responsible for the cycling of nutrients in soils. Impacts of increasing CO_2, both on plant biomass production and on microbial composition and activity, will affect mineralization–immobilization processes. Whitford (1992) hypothesized that increasing CO_2 would lead to greater immobilization of nutrients due to changes in decomposer food webs brought about by increased C/N and C/P ratios of high CO_2-grown plants. Luxmoore et al. (1986) observed increased nutrient retention in the plant–soil system of Virginia pine under high CO_2, but did not determine if this was due to increased plant uptake and/or increased incorporation in microbial biomass. O'Neill et al. (1987a) found an increase in total N and P uptake by yellow poplar seedlings under high CO_2 even though nitrite-oxidizing and phosphate-dissolving bacteria in the rhizosphere were reduced at the final harvest. They speculated that the decline in populations of bacteria was a function of decreased nutrient availability as competition with

seedling roots increased during the growing season. Although 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 (Runion et al., 1994a). Zak et al. (1993) 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 a significant increase in N mineralization that they related to possible increase in turnover rate of microbial N and/or an increased N release from soil organic matter.

The root, the rhizosphere, and associated microorganisms form a complex environment which is vital to the overall health of plants. Changes in atmospheric CO_2 will elicit changes in belowground plant-microbe interactions. Although little is known concerning how CO_2-induced changes in the biosphere will affect the belowground environment, it is recognized as a research area of critical importance and is, of late, receiving increased attention.

SOILS

Highly interesting, but not yet studied, are the implications of global change, CO_2 in particular, for soils. The issue, however, is beginning to receive serious thought (Arnold et al., 1990; Bouwman, 1990; Buol et al., 1990; Hatfield, 1990; Schlesinger, 1991; Coleman et al., 1992; Follett, 1993).

The concentration of nutrients in plant tissues is largely influenced by the capacity of plant roots to mine the soil profile. The effects of CO_2 on roots and other belowground processes will therefore affect whole plant nutrition and may increase root-zone competition for nutrients (Grodzinski, 1992). Whole plant nutrient uptake is increased for many species under elevated CO_2 but the concentration of most nutrients per unit dry weight of tissue is decreased. Elevated atmospheric CO_2 usually increases the size of plants and their component parts, resulting in greater total amounts of nutrients, but these nutrients are distributed throughout the larger plants and thus, the concentration per unit weight is reduced. Also, nutrient use efficiency (unit of biomass produced per unit of nutrient) generally increases under elevated CO_2, while nutrient uptake efficiency (unit of nutrient per unit weight of root) declines in general. Again, under high CO_2, plants are able to produce more biomass with available nutrients but the larger root systems of these plants may not be able to gather additional nutrients in proportion to the increase in their root systems. The results on nutrient uptake and concentration are variable due to differences in nutritional levels applied during the course of the experiments. For example, when plants are grown under nutrient levels considered to be adequate or poor for ambient conditions, exposure to high CO_2 results in larger plants with lower tissue nutrient concentrations (Norby et al., 1986a,b; Yelle et al., 1987). Conversely if plants growing under higher CO_2 are supplied with higher levels of nutrients, concentration of nutrients in tissues and/or nutrient uptake efficiency in general are not significantly affected by the CO_2 concentration (Israel et al., 1990).

In a study of the influences of elevated CO_2 on plant N use, Coleman et al. (1993) observed that decreases in tissue N concentration may not be due to physiological shifts in N use efficiency, but rather are more likely the result of a plant size-dependent phenomenon due to accelerated growth. Sinclair (1992) has discussed the degree of complexity involved in the interactions between atmospheric CO_2 concentration and mineral nutrition, emphasizing the uncertainty associated with them.

Bazzaz and Miao (1993) observed modifications of the CO_2 response in three early-successional tree species (gray birch, white ash, and red maple), a significant growth increase only occurring under a high nutrient regime. They observed enhanced growth of six deciduous tree species under CO_2 enrichment. Lower light, higher nutrients, and larger seeded species favored greater responses. Their study underscores the importance of considering environmental resources in efforts to understand the response of vegetation to CO_2 concentration.

Conroy et al. (1986, 1990, 1992) have considered the effect of CO_2 enrichment on several species. Conroy (1992) concludes that the greatest absolute increase in productivity (as a result of elevated CO_2 exposure) will occur when soil N and P availability is high. Nitrogen shortage does not preclude an elevated CO_2 effect on growth, but in some C_3 plants low P can eliminate a high CO_2 response, the lack of P possibly limiting photosynthesis and root symbiosis. For maximum productivity of C_3 crops, higher P levels will be needed at high CO_2, whereas the N requirement will be lower. This suggests the need to change standard fertilizer recommendations as global CO_2 concentration increases. An important consideration here is the predicted limitation in the future availability of phosphate fertilizer in some developing nations (e.g., in the tropics; Scharpenseel et al., 1990).

Zak et al. (1993) saw a positive feedback between C and N soil dynamics and elevated CO_2 using bigtooth aspen grown on a nutrient-poor soil. In addition to significantly greater rates of photosynthesis, number of roots, root length, and rate of root length extension showed substantial increases. Both total and belowground biomass rose significantly. Under N-limited conditions, 50 to 70% of the biomass was partitioned to roots. A test of N mineralization revealed that soil N availability was enhanced by the elevated CO_2 treatment.

The notion of C sequestering by vegetation with subsequent accumulation in the soil has been repeatedly discussed (Denmead, 1991; Rastetter et al., 1991; Gifford, 1992; Post et al., 1992; Wisniewski & Lugo, 1992; Follett, 1993; Schlesinger, 1993; Wisniewski et al., 1993). Agreement on the environmental sinks (identification, size, and rates) of surplus CO_2 is not in sight nor is there a consensus on the role of soil. In one response to this uncertainty, Harrison et al. (1993) have recently proposed a strategy for estimating the effect of CO_2 fertilization on soil C storage.

With respect to soils, another important aspect is salinity. Plant tolerance to salinity under high levels of CO_2 has been briefly addressed. Salt tolerance appears to rise as CO_2 concentration is increased (Schwarz & Gale, 1984; Bowman & Strain, 1987; Zeroni & Gale, 1989). Ball and Munns (1992) report three general conclusions from the limited salinity/CO_2 response data available: (i) the CO_2 growth response is higher under moderate salt stress than under opti-

mal salinity regimes; (ii) water use efficiency (WUE) usually increases as CO_2 levels are elevated; and (iii) leaf salt concentrations are similar in both high CO_2 treated and untreated plants despite substantial differences in WUE. This is seen in C_3 halophytes and in both C_3 and C_4 nonhalophytes. The authors find that available data imply root/shoot communication in the regulation of salt balance for adjustment to environmental factors that affect water and ion availability at the root and C intake and water loss in the leaf.

Sombroek (1990) has suggested that CO_2-stimulation of root growth combined with increased production of organic matter (and its even stronger decomposition) would lead to an intensification of rock weathering, implying deeper soils with a higher availability of mineral nutrients like K from newly weathered parent material. He goes on to point out that enhanced biomass production would provide better soil cover and hence reduced soil erosion. The weathering of parent soil material is an extremely slow process. If in fact enriched CO_2 and its effects on higher plants lead to accelerated weathering, it simply means faster depletion of soil nutrient reserves and increased human intervention (e.g., fertilizer use), taking into consideration atmospheric deposition of essential elements. This discussion represents an issue of significant uncertainty. Peñuelas (1991) has discussed CO_2 effects on biogeochemical cycles, and Berner (1990, 1992, 1993) has considered the weathering of rocks by CO_2-stimulated plant growth. Berner (1992) concluded that much more work is needed on the role of plants in rock weathering because weathering is of such importance to the long-term C cycle. Such work also would be highly germane to understanding soil genesis and formative processes leading to soil structure.

Increasing levels of CO_2, along with other global changes, will undoubtedly affect soils and soil resources. Work in this area is beginning and must be continued, given the vital nature of soils in agriculture, forestry, and terrestrial ecosystems in general. Thus far, work has been hampered—primarily by inadequate techniques—but, because of recent advances in research methodology, the current outlook is bright.

METHODOLOGY

Our progress in understanding the influence of elevated atmospheric CO_2 on belowground processes depends upon two sets of technology—one is available techniques for elevated CO_2 exposure under field conditions (Strain, 1991; Allen et al., 1992) and the other is methodology for root research in situ (Caldwell & Virginia, 1989; Epstein, 1990; Taylor et al., 1991). To date, progress in the area of belowground research has been limited by the technology. Besides conventional methods used during the past half-century, a number of new approaches have appeared during the last decade. On the horizon are some even more promising advanced technologies. Conventional methods include trench profile, soil coring, root in-growth mesh bags, and various vessels with transparent sides (Böhm, 1979; Neill, 1992). The improvement of these methods have come mainly with the addition of various power assisted sampling tools and new devices for root measurement (Upchurch & Taylor, 1990; Mackie-Dawson & Atkinson, 1991; Prior & Rogers, 1992, 1994). New approaches include neutron

radiographic imaging of root systems (Willatt et al., 1978; Taylor & Willatt, 1983), the use of color video cameras in mini-rhizotrons (Upchurch & Ritchie, 1984; Kaushal et al., 1989; Box, 1993; Hendrick & Pregitzer, 1993), root measurements with image-analyzing computers (Ottman & Timm, 1984; Berntson, 1992), porous membrane root cultures in the field (Brown & Haq, 1984), modified weighing lysimeters for providing profiles of root density and water extraction (Dugas et al., 1985), herbicide banding to screen root genotypes in the field (Robertson et al., 1985), and computer assisted tomography (CAT scan; Hainsworth & Aylmore, 1986; Aylmore, 1993). Tracers including ^{15}N (Knowles & Blackburn, 1993), ^{11}C (Magnuson et al., 1982; Kays et al., 1987), ^{13}C (Balesdent & Balabane, 1992; Leavitt et al., 1994), ^{14}C (Lekkerkerk et al., 1990; Johansson, 1992), and various stable isotope ratios (Rundel et al., 1989; Coleman & Fry, 1991; Wong & Osmond, 1991; Ehleringer et al., 1993; Schimel, 1993) have been used effectively in root studies.

The emphasis in future subterranean work (biological and edaphic) will be on noninvasive, nondestructive access to objects of interest. Among the advanced techniques, yet to be fully developed for subsurface studies, are nuclear magnetic resonance (NMR) imaging (Bottomley et al., 1986, 1993; Kramer et al., 1990), modeling with fractal mathematics (Bartoli et al., 1993; Crawford et al., 1993), optrodes (Angel, 1987; Angel et al., 1991; Munkholm et al., 1988), and synchrotron radiation (Winick, 1987; Schulze & Bertsch, 1993; Schulze et al., 1993). These technologies represent untapped promise for belowground research.

CONCLUSION

In perhaps the best synopsis of the subject to date, Dyson (1992) urges that global change research plans include CO_2 effects on vegetation as a central issue rather than as a mere sideline to climate studies. He aptly points out that the "increase of atmospheric CO_2 may change the conditions of agriculture and plant ecology quite radically, long before any climatic effects become apparent." In his appraisal, Dyson recognizes the comfort and convenience of the warm computer laboratory compared with the muddy, cold winter field site as a driving force in research choices. Level of difficulty is certainly a key consideration for root research in CO_2 field studies. The shear labor inputs under often unfavorable working conditions coupled with a lack of good analytical tools are enough to deter even some experimentalists. Nevertheless, progress is being made. Enough data are currently available to state that belowground processes are indeed responsive to the action of increased CO_2 on plant canopies. Root systems are clearly affected as are microbes in the rhizosphere, and available evidence also suggests certain soil effects *per se*. New research tools promise a much more thorough understanding of belowground responses to elevated atmospheric CO_2.

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APPENDIX

Nomenclature of common and Latin names of plant species

Common name	Latin name
Alfalfa	*Medicago sativa* L.
Amaranth	*Amaranthus* sp.
American bulrush	*Scirpus olneyi* A. Gray
Atlas cedar	*Cedrus atlantica* (Endl.) G. Manetti ex Carrière
Austrian pine	*Pinus nigra* Arnold
Bigtooth aspen	*Populus grandidentata* Michaux
Blue grama	*Bouteloua gracilis* (Willd. ex Kunth) Lagasca ex Griffiths
Broad bean	*Vicia faba* L.
Carrot	*Daucus carota* subsp. *sativus* (Hoffm.) Arcang.
Cassava	*Manihot esculenta* Crantz
Common groundsel	*Senecio vulgaris* L.
Corn (maize)	*Zea mays* L.
Cotton	*Gossypium hirsutum* L.
Curly dock	*Rumex crispus* L.
Gray birch	*Betula populifolia* Marsh.
Konjak	*Amorphophallus konjac* K. Koch
Leek	*Allium porrum* L.
Loblolly pine	*Pinus taeda* L.
Longleaf pine	*Pinus palustris* Mill.
Orchard grass	*Dactylis glomerata* L.
Pea	*Pisum sativum* L.
Peperomia	*Peperomia* sp.
Perennial rye grass	*Lolium perenne* L.
Pineapple	*Ananas comosus* (L.) Merr.
Potato	*Solanum tuberosum* L.
Radish	*Raphanus sativus L.*
Raspberry	*Rubus idaeus* L.
Red maple	*Acer rubrum* L.
Rice	*Oryza sativa* L.
Salt meadow cordgrass	*Spartina patens* (Aiton) Muhlenb.
Shortleaf pine	*Pinus echinata* Miller
Sorghum	*Sorghum bicolor* (L.) Moench
Soybean	*Glycine max* (L.) Merr.
Sugar beet	*Beta vulgaris* L.
Sugarcane	*Saccharum officinarum* L.
Sweet potato	*Ipomoea batatas* (L.) Lam.
Sweetgum	*Liquidambar styraciflua* L.
Tomato	*Lycopersicon esculentum* Mill.
Virginia pine	*Pinus virginiana* Miller
Wheat	*Triticum aestivum* L.
White ash	*Fraxinus americana* L.
White clover	*Trifolium repens* L.

White oak	*Quercus alba* L.
Winter wheat	*Triticum aestivum* L.
Wild radish	*Raphanus sativus* × *raphanistrum* L.
Yellow poplar	*Liriodendron tulipifera* L.

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