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PLANT RESPONSES TO ATMOSPHERIC CO_2 ENRICHMENT WITH EMPHASIS ON ROOTS AND THE RHIZOSPHERE

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Abstract

Empirical records provide incontestable evidence of global changes; foremost among these changes is the rising concentration of CO_2 in the earth's atmosphere. Plant growth is nearly always stimulated by elevation of CO_2. Photosynthesis increases, more plant biomass accumulates per unit of water consumed, and economic yield is enhanced. The profitable use of supplemental CO_2 over years of greenhouse practice points to the value of CO_2 for plant production. Plant responses to CO_2 are known to interact with other environmental factors, e.g. light, temperature, soil water, and humidity. Important stresses including drought, temperature, salinity, and air pollution have been shown to be ameliorated when CO_2 levels are elevated. In the agricultural context, the growing season has been shortened for some crops with the application of more CO_2; less water use has generally, but not always, been observed and is under further study; experimental studies have shown that economic yield for most crops increases by about 33% for a doubling of ambient CO_2 concentration. However, there are some reports of negligible or negative effects. Plant species respond differently to CO_2 enrichment, therefore, clearly competitive shifts within natural communities could occur. Though of less importance in managed agro-ecosystems, competition between crops and weeds could also be altered. Tissue composition can vary as CO_2 increases (e.g. higher C:N ratios) leading to changes in herbivory, but tests of crop products (consumed by man) from elevated CO_2 experiments have generally not revealed significant differences in their quality. However, any CO_2-induced change in plant chemical or structural make-up could lead to alterations in the plant's interaction with any number of environmental factors—physicochemical or biological. Host–pathogen relationships, defense against physical stressors, and the capacity to overcome resource shortages could be impacted by rises in CO_2. Root biomass is known to increase but, with few exceptions, detailed studies of root growth and function are lacking. Potential enhancement of root growth could translate into greater rhizodeposition, which, in turn, could lead to shifts in the rhizosphere itself. Some of the direct effects of CO_2 on vegetation have been reasonably well-studied, but for others work has been inadequate. Among these neglected areas are plant roots and the rhizosphere. Therefore, experiments on root and rhizosphere response in plants grown in CO_2-enriched atmospheres will be reviewed and, where possible, collectively integrated. To this will be added data which have recently been collected by us. Having looked at the available data base, we will offer a series of hypotheses which we consider as priority targets for future research.

Keywords: global change, carbon dioxide, plants, roots, rhizosphere.

INTRODUCTION

The greatest experiment on earth has begun. We are changing the parameters that drive the planet's living systems. Among these is atmospheric CO_2 which emanates from our fire-driven economy. Carbon dioxide is the first molecular link from atmosphere to biosphere. It is essential for photosynthesis which sustains plant life, the basis of the entire food chain. No substance is more pivotal for ecosystems, either natural or managed.

The concentration of CO_2 was 270 ppm before the Industrial Revolution and has risen continuously to more than 355 ppm today. The trajectory of the change in atmospheric CO_2 concentrations, so clearly tracked by C. D. Keeling, is expected to double during the last half of the next century (Bolin *et al.*, 1986). Figure 1 shows the trace of the atmospheric CO_2 concentrations over the past three decades (Keeling *et al.*, 1989). The ever increasing magnitude is the most apparent feature. The recurring saw-toothed pattern is thought to reflect the seasonal cycle of the growth of vegetation in the Northern Hemisphere (Bacastow *et al.*, 1985). In fact, Keeling (1983) has postulated that the observed amplitude increase may be due to the stimulation of terrestrial plant activity. Modelling efforts by Kohlmaier *et al.*

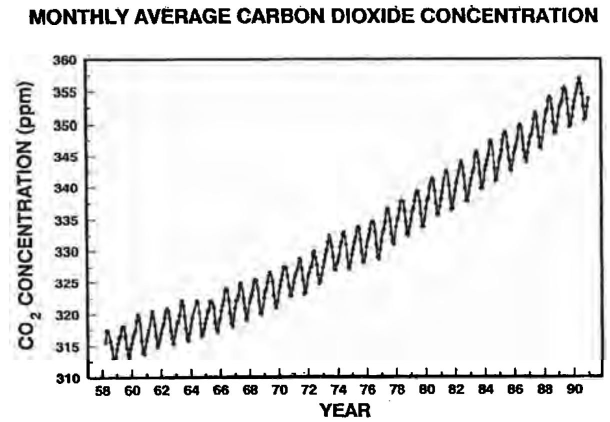

Fig. 1. Original CO_2 concentration data of Keeling *et al.* (1989) including Keeling's latest measurements (Boden *et al.*, 1991) from Mauna Loa Observatory, Hawaii.

(1987, 1989) have suggested that a CO_2 fertilization effect associated with land biota is likely to explain around 25% (range: 8–64%) of the integral amplitude rise in the CO_2 signal from 1958 to 1988. A recent article by Tans *et al.* (1990) lends further credence to the idea of terrestrial ecosystems as sinks for large amounts of CO_2; differences between empirically observed atmospheric levels of CO_2 and surface ocean water partial pressures of CO_2 of the Northern Hemisphere were too small for oceans to be the major sink. These studies point to the inextricable linkage between vegetation and atmosphere.

As a result of the accumulation of CO_2 and other radiatively active trace gases in the troposphere, shifts in climate (temperature and precipitation patterns) have been predicted. Regardless of whether climatic changes take place, plants will be directly affected by the higher CO_2 concentration. Virtually all studies to date have shown enhanced crop growth, alleviation of some types of stress, and substantial increases in yield by elevated CO_2 levels. However, since individual species respond differently, competitive shifts might lead to alterations in the composition, structure, and function of natural plant communities.

Recent reviews integrate and interpret the CO_2 effects literature base (Krupa & Kickert, 1989; Bazzaz, 1990; Kimball *et al.*, 1990; Allen, 1993; Poorter, 1993; Rogers & Dahlman, 1993). Wittwer (1985) has written an excellent historical perspective on the benefits of CO_2 enrichment to plant productivity. Dahlman (1993) has provided a 10-year summary of CO_2-plant effects research. Drake *et al.* (1985) have critically evaluated methods for exposing plants to CO_2. Available field techniques for CO_2 experimentation have recently been described by Strain (1991). Much of our data base has been derived from controlled growth chamber and greenhouse studies; over the past few years assessments have been made with open top chambers in the field, and now FACE (free-air CO_2 enrichment) systems are beginning to come on line (Allen *et al.*, 1993). New stable isotope tracing methodology (Leavitt *et al.*, 1993) and novel approaches such as nuclear magnetic resonance (NMR) imaging (Bottomley *et al.*, 1993) are starting to be used in CO_2 effects work (Rogers & Bottomley, 1987; Rundel *et al.*, 1989). Both these approaches are highly effective since they are non-invasive and may be used *in situ*. Another progressing front is the development of plant/environment simulation models so essential to the efficient use of existing knowledge. Models are indispensable as tools for understanding complex response phenomena and for reliably predicting vegetation reactions to changing conditions.

Here we provide a short overview of the influence of more CO_2 on plants with emphasis on belowground aspects, namely roots and the rhizosphere. First, plant responses—structural and physiological—and their associated interactions will be discussed. We briefly outline the current state-of-knowledge on CO_2 effects, along with a short series of important but unanswered questions. Then published reports of the effects of aerial CO_2 enrichment on root development will be reviewed in detail. The few available studies on the rhizosphere in relation to CO_2-induced changes in plant growth will be presented. Finally, specific targets for future research on belowground processes will be proposed.

STRUCTURE

The effects of CO_2 on plant structure are many. In their study of leaf ultrastructure, Cave *et al.* (1981) reported the accumulation of large starch grains in the chloroplasts of clover.† Vu *et al.* (1989) observed similar starch deposits in soybean, but no appreciable alteration of chloroplast structure. The expanse and thickness of leaves increase (Apel, 1989). Observations of soybean leaf cross sections have revealed three layers of palisade cells for CO_2-enriched treatments (up to 910 ppm) rather than two as under ambient (340 ppm) CO_2 (Thomas & Harvey, 1983). Shifts in stomatal density have also been seen. Thomas & Harvey (1983) saw no significant influence of CO_2 on the stomatal indices of corn, soybean, or sweetgum. Woodward (1987), in an examination of herbarium leaf specimens of eight temperate arboreal species collected over the last 200 years, observed a 40% decrease in stomatal density. Experimental studies within the CO_2 concentration range of 225–340 ppm were consistent with this finding (Woodward & Bazzaz, 1988). However, Apel (1989) in a comparison of nine species grown at either 345 or 1500 ppm reported a significant increase in stomatal density; a large difference in response was observed among 12 French bean cultivars, with an average rise of 36%. Increasing CO_2 leads to a rise in stomatal density of rice leaves, largely as a result of more stomata per row, although on the abaxial surface also more rows across the leaf (Rowland-Bamford *et al.*, 1990). Perhaps this differential response across studies is species dependent or related to experimental

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† For the Latin names of various plant species, the reader is referred to the Appendix.

conditions, such as exposure to sudden elevations of various CO_2 concentrations.

Individual plant organs have often been observed to enlarge proportionally with added CO_2. Significantly higher leaf areas have been recorded (Rogers *et al.*, 1983*a*; Gifford, 1988). Lengths of stems and number of nodes increase (Allen *et al.*, 1990*a*). Enhanced numbers of specific parts (stems, branches, tillers, and flowers) are common. For soybean, emergence and expansion rates of main stem leaves increase at high CO_2 (Cure *et al.*, 1989). Reproductive structures (which are often the marketable product) may increase in size or number (Acock & Allen, 1985).

A so-called 'luxury consumption' of carbon can occur when extra CO_2 from the air is available. This can translate into plant parts with higher densities than might actually be required (Acock & Allen, 1985). This can also lead to taller, denser canopies and greater root length densities. Such changes may enhance the plant's capacity to harvest light, water, and nutrients. Practically speaking, this capacity to gather raw materials can become crucial over the cropping cycle or within the life of natural communities.

ENERGETICS

Figure 2 provides a schematic representation of energy producing and energy consuming metabolic processes in plants. At the photosynthesis level, there are three main plant groups, so-called C_3, C_4, and CAM (Crassulacean acid metabolism) plants. Three and four refer to the number of carbon atoms in the first molecules formed at the end of the initial CO_2 fixation pathway. Soybean, wheat, rice, and potato are examples of C_3 plants. The C_4 pathway is found in tropical grass crops like corn, sugarcane, sorghum and some members of the families Chenopodiaceae and Amaranthaceae. The C_4 type metabolism is almost never found in woody species. The C_4 plants are more efficient in photosynthesis than the C_3 plants. In C_3 plants, 20–50% of the carbon fixed is immediately lost by photorespiration. In contrast C_4 plants exhibit little photorespiration. In comparison to these two types, 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. CAM plants include such species as pineapple and succulent vegetation like cacti and stonecrops (e.g. *Sedum*); they are highly efficient users of water.

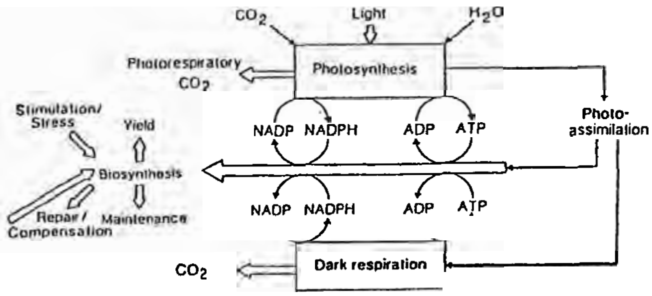


Fig. 2. Energy producing and energy consuming metabolic processes in plants (modified from Kosuge and Kimpel (1981); reproduced by the kind permission © of the Cambridge University Press).

The photoassimilated carbon and the generated energy are utilized toward biosynthesis. A portion of such biosynthesis constitutes the maintenance costs for the plant. In addition, plants must also expend energy when required for stress compensation or repair. In the end, the observed biomass yield is due to: [[any stress effect] – [repair]] + [maintenance]. If stress exceeds repair, (excluding the normal maintenance costs) then there will be an adverse effect on yield. To the contrary, if repair exceeds stress, there will be no adverse effects. Elevated CO_2 concentrations essentially act as stimuli facilitating biosynthesis to exceed the maintenance and any stress repair costs, leading to higher plant biomass.

PHOTOSYNTHESIS

High levels of CO_2 stimulate photosynthesis, particularly in C_3 plants. This is caused by the higher CO_2 *per se*, since both CO_2 and O_2 compete for the same site on the catalyzing enzyme rubisco (ribulose-1,5-*bis*-phosphate carboxylase) (Goudriaan *et al.*, 1990). The C_4 types are much less affected since photorespiration is already suppressed by a CO_2-concentrating mechanism (Poorter, 1993). Figure 3 illustrates the classic C_3 and C_4 photosynthetic responses. The C_4 are quickly saturated as CO_2 concentration rises, while in the C_3 species photosynthetic responses continue to rise across a range extending over several hundred ppm 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). A substantial amount of work has focused on net photosynthesis at higher concentrations of CO_2 (Huber *et al.*, 1984*a,b*; Gifford & Morison, 1985; Radin *et al.*, 1987; Allen *et al.*, 1990*b*; Besford *et al.*, 1990). Critical reviews of this topic have recently been published (Bowes, 1991; Long & Drake, 1992).

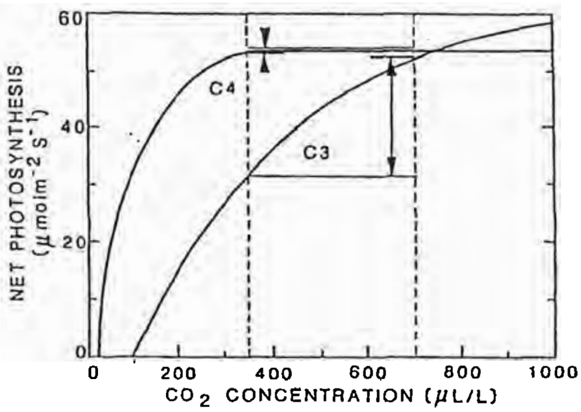


Fig. 3. Classical net photosynthetic curves for C_3 and C_4 species (Taiz & Zeiger, 1991). Dashed vertical lines at 350 and 700 μl/litre mark the current CO_2 level and the doubled concentration predicted to be reached sometime late in the next century (Houghton *et al.*, 1990). Arrows indicate incremental rise in net photosynthesis due to the CO_2 doubling (Kimball *et al.*, 1993).

Despite well-known plant growth enhancements, the idea of photosynthetic acclimation leading to little or no long term gain in growth has been repeatedly examined (Delucia *et al.*, 1985; Peet *et al.*, 1985; Sasek *et al.*, 1985; Tissue & Oechel, 1987; Sage *et al.*, 1989). 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. In his recent discussion, Drake (1992) 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 investigators, however, even when showing photosynthetic reductions, have observed that the rates of photosynthesis are sustained significantly above those expected under present day ambient CO_2 conditions. In general, the effect of elevated CO_2 on photosynthetic capacity is still uncertain. Considerations of sink activity (i.e. carbon partitioning among the various plant organs) may help interpret divergent findings (Cure *et al.*, 1987, 1991; Herold, 1980; Drake, 1992). In fact, recent studies have shown a strong correlation between pot size and photosynthetic capacity (Arp, 1991; Thomas & Strain, 1991). Such results suggest a need to carefully consider rooting volume in CO_2 response studies.

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. Up to 50% of carbon fixed in C_3 plants may be lost due to respiration (Farrar, 1985; Amthor, 1989). Although few studies have attempted to determine the role of CO_2 on 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 carbon content. This may increase the energy cost of constructing foliage per unit area. Conversely, leaf protein and nitrogen content tend to decrease with increasing CO_2 (Cure *et al.*, 1988*a*). Proteins have a high construction cost and increased protein content is associated with increased maintenance costs due to turnover; therefore, total costs of tissue construction and maintenance may be decreased with CO_2. Carbon dioxide increases in the atmosphere tend to increase root growth more than aboveground growth (Wittwer, 1978; Prior *et al.*, 1993). Since respiration of roots is significantly greater 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 has also been hypothesized that, since respiration rates of fungi are higher than for vascular plants, increased mycorrhizal colonization of plant roots under elevated CO_2 may increase whole-plant respiration (Lamborg *et al.*, 1983). 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). Respiration, particularly cyanide resistant respiration (Lambers, 1985), can increase as nonstructural carbohydrates increase. Since additional CO_2 can increase the concentration of nonstructural carbohydrates (Amthor, 1988), another mechanism exists which could account for an effect of CO_2 on plant respiratory costs. The biochemical bases for respiratory responses to ethylene are unclear; however, ethylene is a strong promoter of respiration and CO_2 can affect 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). 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, *Amaranthus*. 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 25–30%, while a decrease in CO_2 elicited a corresponding increase in respiration (Amthor, 1988). Implications of these phenomena for real world plant systems will have to await further research. Such findings may call for a redesign of some of the 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 nitrogen content. In particular, separating the effects on the functional components of respiration (i.e. construction, maintenance and ion uptake) as well as carbon costs due to root exudation are needed. These gaps in our knowledge hamper the development of adequate models that assess the response of plant respiration to CO_2 and represent major uncertainties as to the effects of CO_2 on the carbon cycle.

WATER USE

At the cellular level, elevated CO_2 slows transpiration rate by inducing the partial closure of guard cells that form stomates on leaf surfaces (Jones & Mansfield, 1970). This contributes to an increase in water use efficiency (WUE, the ratio of carbon fixed to water transpired). Physiologically, WUE increase represents one of the most significant plant responses identified thus far, to excess CO_2. Both the suppressed use of water and the rise in photosynthetic rate go toward pushing this important ratio upwards. Relative percentage contributions of the two processes in the C_4 species corn is 27:73 (net photosynthesis:transpiration rate) while in the C_3 plant soybean, it is 90:10 (Acock &

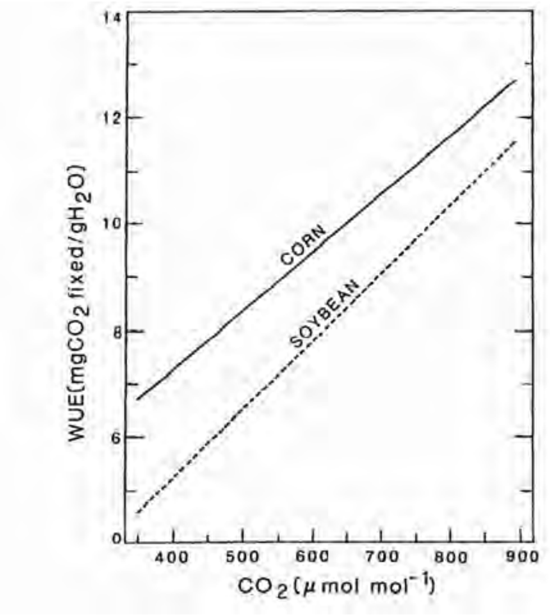


Fig. 4. Water use efficiencies for corn and soybean over a range of CO_2 concentrations. Values were fitted by the method of least squares regression and are based on 50 observations for corn and 46 for soybean, both grown at 340, 520, 718 and 910 ppm.

Allen, 1985). In the C_4 plant, the transpiration component is far more important than in the C_3. Figure 4 shows WUE for field-grown corn and soybean over a range of CO_2 concentrations (Rogers *et al.*, 1983*b*). That WUE is increased by CO_2 enrichment has often been reported (Sionit *et al.*, 1984; Morison, 1985; Baker *et al.*, 1990*c*); however, discrepancy does exist. Some reports indicate that larger plant size (leaf area) counterbalances the reduction in water use, offsetting enhanced WUE (Allen, 1993). Data shown in Fig. 5 indicate that WUE is highest with elevated CO_2 and low LAI (leaf area index), while the lower CO_2 level and high LAI resulted in the lowest WUE. Others suggest that the landscape's response is not adequately reflected by studies of small numbers of plants in artificial enclosures. Rosenberg *et al.* (1990) have examined the potential effects of climate and CO_2 enrichment on evapotranspiration. At least one recently completed simulation, which included climate change, found that under certain conditions a decrease in evapotranspiration could be expected (Kuchment & Startseva, 1991), while another (Curry *et al.*, 1990) predicted a rise in plant water needs. By and large, most studies have reported enhancements. In their comprehensive treatment of the topic, Kimball and Idso (1983) cited 46 observations which cumulatively showed that transpiration would be lowered by an average of 34% which, coupled with an economic yield enhancement of 33% (over 500 observations), suggested a doubling of water use efficiency for a doubling of CO_2 level.

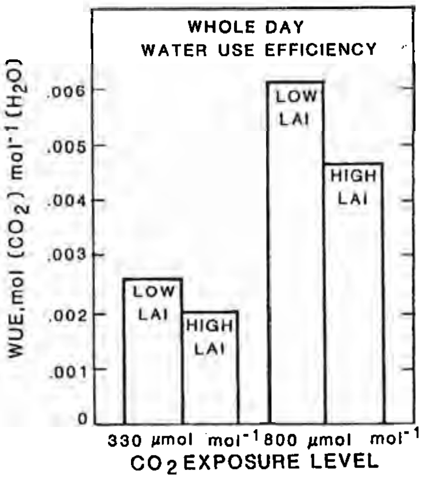


Fig. 5. Whole day water use efficiencies (WUE) of soybean canopies grown at a daytime dry bulb air temperaure of 31°C and a dewpoint temperature of 21°C. Low leaf area index (LAI) was 3·3 and high was 6·0 (Jones *et al.*, 1985).

No in-situ, non-invasive field studies of CO_2 effects on plant water use have been published to date. In the field, water availability will depend upon rainfall distribution, leaf and canopy structure, extent and depth of rooting, and the various weather variables. For an accurate assessment, field tests of indigenous species unencumbered by experimental equipment (i.e. micrometeorology must be normal) will have to be performed.

INTERACTIONS WITH OTHER ENVIRONMENTAL FACTORS

Virtually any factor that affects plant growth can influence its reaction to elevated CO_2 (Fig. 6). From a different vantage point, it is also known that CO_2 can ameliorate certain environmental stresses. The role of CO_2 as a chief input to plant life may become especially significant in view of predicted future climate effects on vegetation (Bolin *et al.*, 1986; Idso, 1989). Water, temperature, light, nutrients, salinity, and air pollutants have all been observed to interact with CO_2-induced responses. In addition, biological interactions with crops have been seen in the form of altered weed competition

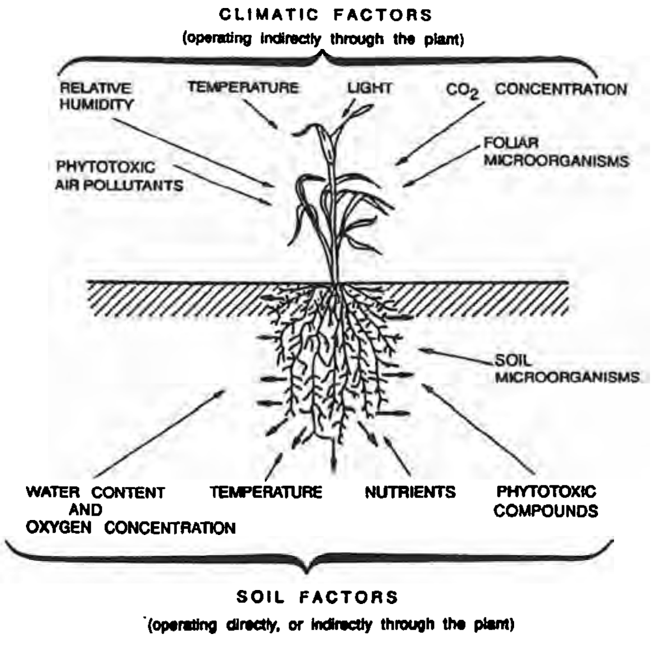


Fig. 6. Climatic and soil factors (biotic and abiotic) affecting activity of the root system (modified from Dommergues, 1978).

and insect pests relationships. Microorganisms, including diseases, associated with plants could also be affected.

Water stress has been repeatedly observed to be ameliorated by increased concentrations of CO_2 (Gifford, 1979; Sionit *et al.*, 1980, 1981*d*; Morison & Gifford, 1984*a,b*; Schonfeld *et al.*, 1989). We have observed this with soybean (Rogers *et al.*, 1984; Prior *et al.*, 1991). Figure 7 shows architectural diagrams of soybean plants grown at three CO_2 levels under both well-watered and water-stressed conditions in our laboratory (Prior, 1986). Growth enhancement by CO_2 and a water stress compensating effect may be readily noted. Reports that this stress is decreased in other plant species are not uncommon (Wong, 1980; Lemon, 1983; Acock & Allen, 1985; Goudriaan & Bijlsma, 1987; Nijs *et al.*, 1989). By inducing the partial closure of stomates, water is conserved. To date the role of plant roots, the primary extractors of soil water, has not been elucidated in the present context. This phenomenon of protection from water stress could help alleviate negative impacts of drier future climates.

Baker and Allen (1992) substantiated a high degree of temperature dependence in soybean growth response to elevated CO_2. Jones *et al.* (1985) have provided response curves for photosynthesis and transpiration under various levels of both CO_2 and temperature. Idso *et al.* (1987) reported results suggesting that for a 3°C rise in mean surface air temperature plant growth enhancement would increase from 30 to 56%. Their results also showed that at cooler temperatures (<18·5°C, daily mean) elevated CO_2 tended to reduce plant growth. The authors aptly pointed out that this temperature dependence would make the prediction of CO_2 response far more complex than first thought. Both Potvin (1985) and Sionit *et al.* (1981*b*) saw alleviation of chilling effects by CO_2 enrichment. Potvin observed a buffering of physiological shifts due to cold, whereas Sionit *et al.* saw an elevated CO_2 compensation for chilling in the garden vegetable okra. The life cycle of the plant could be completed at a temperature several degrees lower with added CO_2. Overall, interaction of CO_2 and temperature is not well understood; there is some conflict in the experimental data base.

Light and CO_2 have long been known to interact; both affect the plant through the photosynthetic process. Brun and Cooper (1967) have provided a full spectrum of light and CO_2 interactions with soybean leaves. They found that after maximum net photosynthesis was reached, it declined if either light level or CO_2 concentration was lowered. Sionit *et al.* (1982) reported similar findings for soybean, radish, sugar beet, and corn; total dry matter production was highest at the highest values of CO_2 and light tested. It has been concluded that, at least in part, elevated CO_2 can compensate for reduced light (Hurd, 1968; Acock & Allen, 1985; Mortensen & Ulsaker, 1985).

Positive plant response to CO_2 appears to occur under a wide range of nutrient availability (Sionit *et al.*, 1981*a*; Sionit, 1983; Cure *et al.*, 1988*a,b*). Studies (with soybean, corn, rice, cotton, wheat, and a few weed species) have, however, demonstrated diminished growth responses due to nitrogen limitation (Goudriaan & de Ruiter, 1983; Cure *et al.*, 1988*a*). One study has shown this with several plant types over a range of dilutions of a complete nutrient solution (Patterson & Flint, 1982): that is, with increasing nutrient availability, the CO_2 stimulation response appears to grow larger.

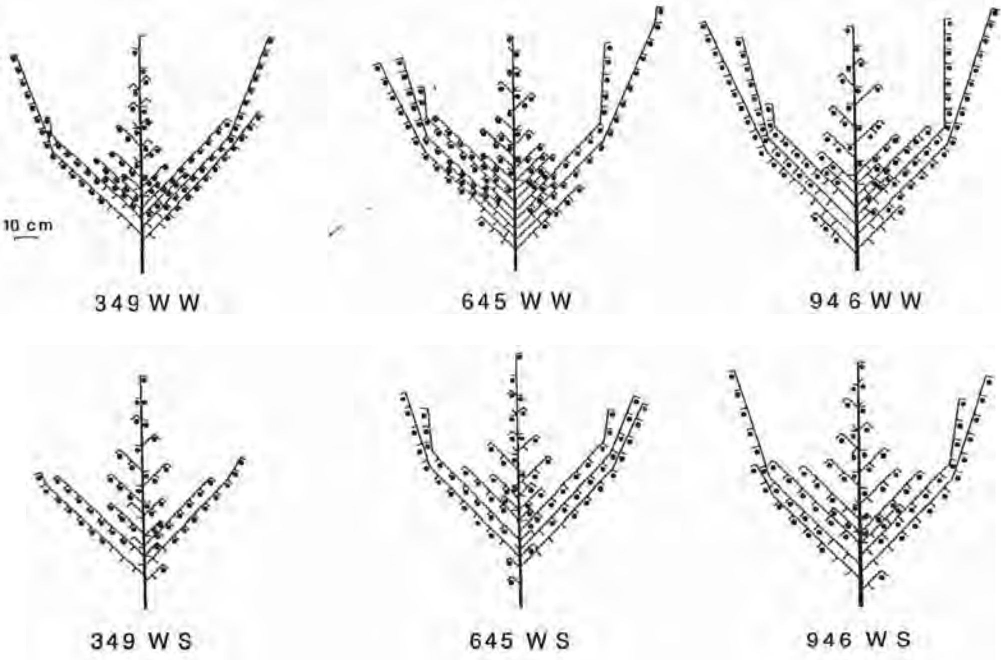


Fig. 7. Plant architectural diagrams of well-watered (WW, rewatered at −0·010 ± 0·005 MPa) and water-stressed (WS, rewatered at −0·080 ± 0·0045 MPa) soybean indicating mean morphological data during late pod fill stage of growth for plants grown at CO_2 concentrations of 349, 645 and 946 ppm. Diagonal lines represent sum of lateral branch lengths at each node; short perpendicularlines are leaves; dots equal two pods; replicate number per treatment was six; and scale mark is 10 cm (Prior, 1986).

Relief from the effects of salinity has been seen in some studies (Schwarz & Gale, 1984; Bowman & Strain, 1987). In other words, salt tolerance increases as CO_2 concentration goes up (Zeroni & Gale, 1989). There are two possible explanations. Extra supplies of photosynthate may help to offset increased respiration demands. Less water throughout in the transpiration stream (rate lowered by extra CO_2) could lessen the quantity of salt taken up (Acock & Allen, 1985).

The narrowing of stomates by increased levels of CO_2 immediately infers the possibility of protection from air pollutants that enter leaves by this route. In fact this has been experimentally demonstrated, and briefly discussed by Morison (1988). A few investigators have shown a lessening of injury by O_3, SO_2 NO, and NO_2 on several common crops (Hou *et al.*, 1977; Carlson & Bazzaz, 1982; Reddy *et al.*, 1989*b*; Allen, 1990). Allen's recently published review (1990) of the topic revealed a paucity of data and concluded further studies were needed.

Weeds are important since they suppress crops in a variety of ways by competing for vital resources. The differential responses of plant species to rising CO_2 suggest that relative competitiveness may be altered. This has been found to be the case. Studies by Patterson and Flint (1990) have shown that weeds with the C_3 pathway would probably outcompete C_4 crops but that C_4 weeds would be less competitive against C_3 crops. Other studies have substantiated this finding (Patterson *et al.*, 1988; Sasek & Strain, 1989). Zangerl and Bazzaz (1984) have noted an unusually high stimulation of growth in the common C_4 weed *Amaranthus*. Potential shifts in weed growth will be important in terms of farm practice and economics.

The interaction of high CO_2 and plant insect pests has been shown (Osbrink *et al.*, 1987; Fajer *et al.*, 1989). Lincoln *et al.* (1984) showed that insect (butterfly larvae) feeding rates rose as CO_2 in the plant growth atmosphere was increased. This was related to the nitrogen and water content of soybean leaves. More recent studies have suggested that leaf-feeding caterpillars do not do as well on plants grown at high CO_2, presumably due to increased carbon:nitrogen ratio (nutritive value lower) (Akey & Kimball, 1989).

Surfaces of plant parts which attract and interact with microorganisms can be expected to change as CO_2 changes the quantity and quality of metabolic products that go to form surface constituents. The manner in which increases in atmospheric CO_2 affect the major diseases of the world's crops may result in positive or negative impacts on crop health and productivity. Generalities regarding effects of CO_2 on host–pathogen interactions can be theorized using knowledge of ecophysiological differences among pathosystems. Elevated CO_2 generally promotes plant growth and, as plant structure is modified, the affected plants may sustain a higher level of infection without reduction in yield. Plants which are more vigorous are able to resist infection from weak pathogens, such as facultative parasites, resulting in lower disease incidence and severity. However, larger plants provide more surface area for infection, and diseases (particularly those caused by obligate parasites) may increase in incidence and severity.

Elevated CO_2 may benefit plant health and productivity by altering the morphology and physiology of plants to the detriment of pathogenic microbes. Growth of soybean at enriched CO_2 concentrations has resulted in the increased deposition of epicuticular wax on leaves and extra layers of epidermal cells (Thomas & Harvey, 1983); this could have important implications for phylloplane dwelling organisms, including pathogens. Lower concentrations of nitrogen, altered C:N ratios, and production of more defense related compounds such as phenolics (Mellilo, 1983) may also lead to lower levels of foliar disease. However, starch and sugar content of plant leaves also have been shown to increase under elevated CO_2 (Yelle *et al.*, 1989), which may provide pathogenic microbes additional substrate for increased growth and reproduction. Thompson (1990) related lower powdery mildew (*Erysiphe graminis*) infection of wheat seedlings under elevated CO_2 to reductions in leaf nitrogen; he also reported that the effects of CO_2 on this pathosystem were influenced by the water status of the wheat seedlings. Thompson and Drake (1993) related lower severity of a foliar rust disease of a C_3 sedge under elevated CO_2 to reductions in leaf nitrogen content, but attributed an increase in foliar disease severity (fungus unknown) under elevated CO_2 for a C_4 grass to increased leaf water content. Runion *et al.* (1993) found that populations of various fungi on cotton leaves were differentially affected by elevated CO_2, but no appreciable effect of CO_2 on phylloplane bacteria or actinomycete populations was observed.

Changes in atmospheric CO_2 will elicit complex changes in plant-microbe interactions (Idso, 1990). Plant diseases will vary depending upon the host, the microorganism, and the environmental factors, all of which may be altered by an elevated CO_2 atmosphere. However, little is known to date concerning the role of CO_2 in this vital aspect of plant health.

AGRO-ECOSYSTEMS

Major world crops have been researched to varying degrees with respect to CO_2 effects (Cure & Acock, 1986; Enoch & Zieslin, 1988; Warrick, 1988; Kimball *et al.*, 1989; Newman, 1989; Smith & Tirpak, 1989; Enoch, 1990). A brief summary of known direct effects of elevated CO_2 on crops is given in Table 1, and an overview of possible interactions with other environmental variables in Table 2. Table 3 presents some key unresolved issues. The contents of these tables are based on interpretation of the literature base by Rogers *et al.* (1992*a*).

Faster growth and earlier maturity of crops are possible consequences of rising CO_2. Acceleration of development and a shortening of total growth duration have been recorded for rice (Baker *et al.*, 1990*b*).

Table 1. Direct effects of elevated CO_2 concentrations on crops: A general summary of what is known

Parameter	Effect	Comment
1 Photosynthesis and growth	Stimulation	In most cases
2 Photosynthetic capacity	Reduction	In a few cases in long-term exposures, under some conditions and not others
3 Stomatal conductance	Reduction	By ~40% at 2*X* present CO_2 concentrations
4 Structure and physiology	Marked alteration	Larger plants, starch and sugar accumulation
5 Water use efficiency	Increase	~2*X* at 2*X* present CO_2 concentrations
6 Water use per unit leaf area	Reduction	Significant at high CO_2. Reduced loss per unit land area due to larger leaf area
7 Foliar composition	Marked alteration	Increased C : N ratio under high CO_2
8 Maturation rate	Increase	In many cases early flowering under high CO_2
9 Biomass yield	Increase	By as much as 200% in young, widely spaced crops (e.g., citrus)
10 Economic yield	Increase	By ~33% in C_3 plants (e.g., soybean, wheat, potato) and by ~10% in C_4 plants (e.g., maize, sorghum, sugarcane) at 2*X* present CO_2 concentrations

Mauney *et al.* (1993) found that cotton grown under free-air CO_2 enrichment attained maturity (with respect to economic yield) five weeks sooner than controls. Calvert (1972) reported earlier ripening of tomato. Our work with soybean at elevated CO_2 showed that physiological maturity was attained four days earlier and the general senescence that followed progressed even more rapidly (Rogers *et al.*, 1986). A decrease in the time to produce a crop would be of enormous importance in regions where growing seasons are already of marginal length or in areas where double cropping is practiced.

Economic yield, the bottom line of all farming, has been seen to increase. Kimball's (1983*a*,*b*) excellent compilations and analyses of hundreds of prior studies suggest an enhancement factor of 1·32 (99·9% confidence interval: 1·24–1·43) if ambient CO_2 were doubled. Virtually all authors dealing with direct effects of CO_2 have concluded that the impact on the yield of crops will be positive.

What of crop quality? A few investigators have examined this issue. In a study of sudan grass quality, Akin *et al.* (1993) found that enriching CO_2 concentration to 550 ppm in the open field did not reduce forage digestibility, and that CO_2-induced yield increases might be expected to produce biomass of equal bioavailability. Sweet potatoes grown at various enhanced CO_2 levels were identical based on consumer scores of sensory perception (Bhattacharya, 1993). In our work with soybean and corn over a CO_2 range from 340 to 910 ppm, no appreciable effects were observed for percentages of moisture, fat, protein, or crude fiber in seeds (Rogers *et al.*, 1983*a*). Havelka *et al.* (1984) reported no change in the protein content of wheat grown at high CO_2 levels. While shoot nitrogen has generally been observed to decline, seed nitrogen content remains unchanged (Newton, 1991). Interactions between the level of plant nutrition and CO_2 have been suggested.

Increased atmospheric CO_2 is an important aspect of future agro-ecosystems. Farmers, growers, and producers of foods are expected to adjust their practices to best take advantage of this CO_2 subsidy. Based on current projections, there is every reason to believe that this will occur.

One example where agricultural and natural ecosystems meld is in the rangelands that are used for livestock grazing. Earlier this year, Owensby *et al.* (1993*a*,*b*) provided two papers discussing the first and only study of rangeland/grazing responses to elevated CO_2. In their reports, rangeland biomass was observed to increase with extra CO_2 but individual species response varied, suggesting that over time community composition might shift. The methodology needed to investigate grazing of CO_2-affected rangeland was developed. With rangelands occupying over 47% of the world's land area, such research is indeed important.

Forest systems form another continuum between natural and managed plant communities. Individual species have been studied, and increased biomass production under elevated CO_2 is generally observed (refer to Table 4, Forest Ecosystem Components for references). Eamus and Jarvis (1989) reported, with 60

Table 2. Effects of elevated CO_2 concentrations on crops: Possible interactions with other environmental variables

Interacting variable	Comment
1 Temperature	(a) Positive CO_2 effect with rise in °C (b) More water required per unit land area with rise in °C (c) Flower and seed development decreased with rise in °C beyond the normal range of adaptation for each species. For tropical rice, seed yields linearly decrease 10% per °C from 26°C to 36°C regardless of the CO_2 level
2 Drought, salinity, chilling	Reduction in stress response
3 Mineral stress	Reduction in response to elevated CO_2
4 Air pollutants	Reduction in stress response
5 UV-B	Reduction in stress response
6 Insects	Qualitative and quantitative changes in herbivory. More foliage consumed
7 Pathogens	Marked alterations expected with the incidence of both foliar and root diseases, with rise in CO_2 and °C

Table 3. Effects of elevated CO_2 concentrations on crops: Some unresolved issues

1 What are the nature and rates of adaptation of crop species to rising ambient CO_2 concentrations from the past to the present? How will these characteristics influence or modify the predictions of future responses to elevated CO_2 levels

2 Why do some C_3 crop species (e.g. soybean, potato, cotton) maintain or increase their photosynthetic capacity when exposed to long-term elevated CO_2 levels, while others (e.g. rice, cabbage, kidney bean) decrease their capacity? How will this impact crop production?

3 What is the basis for the large range of values for decreases in water use under elevated CO_2 levels? Are these differences related to the climate and/or the experimental regimes?

4 How should the genetic potential for the adaptation of various crop species (in monocultures and in mixtures as appropriate) to changing climate be assessed? What are the relationships between the present geographic ranges of various crop species and the corresponding variability in various growth limiting climate variables (both physical and chemical parameters)?

tree species, an average increase in biomass of 40% for a doubling of CO_2, which is very similar to the increase in yield reported for agronomic crops (Kimball, 1983*a,b*).

Differential responses to CO_2 enrichment among tree species have been observed (Williams *et al.*, 1986) and, thus, one result of rising levels of CO_2 might be to increase the competitive ability of certain tree species relative to others (Bazzaz *et al.*, 1990). Tolley and Strain (1984*a*) found that sweetgum seedling response to high CO_2 was much greater than for loblolly pine seedlings. They further reported that this differential response was enhanced under drought stress and proposed that a doubling of CO_2 would enable sweetgum to become established on drier sites currently dominated by loblolly pine. This differential response may serve to alter species composition and reduce diversity in forests. The impacts this differential response to CO_2 will have on forests will depend on site productivity (Pastor & Post, 1988), their current species composition (Williams *et al.*, 1986) and on their location along the natural to managed plant community continuum, i.e. natural, unmanaged forest ecosystems may be seriously impacted but alterations in species composition will have little or no effect for intensively managed, monoculture tree farms.

Shugart and Emanuel (1985) have underscored the uncertainty of forest response to the direct effects of increased CO_2. Extrapolation of data from past studies, which have generally been of relatively short duration using potted tree seedlings, to actual forest responses must be made with caution (Jarvis, 1989) and direct effects of excess CO_2 on forest themselves have not yet been studied. However, attempts to do so using a new exposure method, FACE (free-air CO_2 enrichment), are underway (Hendrey, 1992).

NATURAL PLANT COMMUNITIES

Natural ecosystems are critical components of the earth's biosphere and the effects of increasing levels of CO_2 on these communities have been considered (Strain & Cure, 1985, 1986; Mooney, 1991; Mooney *et al.*, 1991). Unmanaged plant systems in the wild have a high degree of diversity and complexity, confounding our understanding of their function. It is not surprising that much less is known about natural communities compared with cropping systems. Environmental interactions such as herbivory become all the more important since there is no selective control by man. Strain (1987) has discussed the physiological and ecological aspects of plant response to elevated atmospheric CO_2. His argument, that if primary physiological shifts (in photosynthesis, respiration, and water use) occur, then higher level ecological alterations (in competition, plant–animal relationships, and biotic–abiotic interactions) will take place, is a good one.

In a report of experimental findings, Bazzaz *et al.* (1985) offer some key points concerning plant community response to elevated atmospheric CO_2: (1) differential response by species suggests alteration of competitive relationships, (2) reproductive changes may not follow biomass responses, so full life cycle studies are essential, (3) since flowering and fruiting can shift, some effects may require several generations to be fully realized, and (4) increased CO_2 may offer at least some protection against air pollutants.

Bazzaz (1990), in a major review, concluded that impacts on ecosystem productivity would result primarily from changes in species composition brought about by differential species response to elevated CO_2. Plant density, identity, and proximity, environmental resource availability and the influence of herbivores, pathogens, and symbionts have been found to play crucial roles in the way plants respond to CO_2 enrichment. Bazzaz points out, and rightfully so, that our sketchy knowledge of the highly complex interactions severely limits our prediction of community response to future conditions. In a later report, Bazzaz and Fajer (1992) argue very strongly that CO_2 may greatly alter ecosystem structure and function and that these changes will not necessarily benefit all plants.

In their paper on elevated CO_2 effects on natural plants and plant systems, Woodward *et al.* (1991) conclude that generalities may not be reached since there is a broad range of available experiments, but with differing conclusions and unexpected effects. They suggest that response studies be conducted at the community level with extrapolation back to the plant level rather than the reverse which is so much more difficult.

Wray and Strain (1987*a*) studied competition in old-field perennials at higher atmospheric CO_2 levels. Their results indicate that aster (C_3) becomes a more aggressive competitor against broomsedge (C_4). In a further study of age and competition with these same species it was suggested that future rises in CO_2 levels may decrease the rate of succession in old fields but not necessarily eliminate competition from the community, with a definite potential, however, for shift in competition (Wray & Strain, 1987*b*).

As seen earlier, plant structure may be markedly altered. Shifts in overall form may be of much less consequence to crop production where the rule is monoculture than in natural ecosystems which are highly diverse. Natural interspecific competition is intense and is strongly influenced by canopy architecture, root distribution, and environmental conditions. Harsh stresses are common in these native plant communities, and any amelioration by rising CO_2 or other factors could become highly significant in shifting the competitive balance. In addition, stresses found in natural communities may lessen the impacts of CO_2. For instance, as nitrogen becomes more limiting, one may expect that the response to CO_2 would be dampened.

To a large extent, mechanistic CO_2 work has focused on the influence of variable CO_2 concentration on photosynthetic rates. However, unit leaf area rates of photosynthesis rarely correlate with increases in whole plant growth (Amthor, 1989). Whole plant growth is determined not only by net carbon assimilation per unit leaf area but also by the distribution of carbon among tissues (Norby *et al.*, 1992), the demography of plant organs (rates of birth and death), carbon costs of constructing tissues, and costs required to maintain these tissues. At the community level the distribution of carbon within tissues, particularly roots (e.g. secondary roots versus fine roots, shallow roots versus deep roots), exudation of carbon (see Rhizosphere) and associated feedback relationships, carbon:nitrogen ratio, leaf quality relative to herbivory, and the production of defense compounds may all affect higher order community interactions. Due to these interactions, the efficiency with which carbon gain, at the community level, per unit of resource (i.e. light, water, nutrients) acquired may not easily transcend scale. Instantaneous photosynthetic resource use efficiency may be largely irrelevant at higher organizational scales, yet our understanding and models, of plant communities in the past have in the main, if not exclusively, been predicated on this paradigm.

Different species respond differently to increasing CO_2. This is a chief concern with respect to natural plant community response (where competition governs composition) to global CO_2 rises. It is not so much an issue in crops, except for weeds which must be controlled.

ROOTS

During the past few decades approximately 1000 studies have examined the effects of CO_2 on plants (Kimball, 1983*b*), of which a small portion have included consideration of plant roots (Table 4). Root responses to CO_2 have been studied on a wide diversity of plant species; of the approximately 150 species studied, agronomic and natural community species comprise 30% each with forest species and horticultural crops each contributing 20%. However, the majority (≈61%) of CO_2 studies containing root data have been conducted using agronomic crop plants. Many of the environmental factors discussed previously (i.e. water, temperature, light, nutrition, salinity, air pollutants, and competition) have been demonstrated to have significant interacting effects with CO_2 concentration on root responses for numerous species (Table 4). Variability in plant root response to interacting effects of CO_2 with other factors are primarily due to species variability as well as the levels of the treatment variables being researched.

The most frequently examined root response to elevated CO_2 has been dry weight which was examined in approximately 50% of the studies containing root data. Virtually all studies (≈87%) found that root dry weight increased under elevated atmospheric CO_2 regardless of species or study conditions (Table 4). Roots often exhibit the greatest relative dry weight increase among plant organs under high CO_2 (Wittwer, 1978; Rogers *et al.*, 1983*a*; Imai *et al.*, 1985; Norby *et al.*, 1992) or, similarly, an increase in biomass partitioning to roots (expressed as an increase in the percent dry matter in roots) is sometimes observed (Imai & Murata, 1976; Hocking & Meyer, 1991). This preferential biomass partitioning to roots should result in an increase in the *root to total shoot ratio* (R:TS) which was found to occur in ≈41% of the studies examining this response variable. However, results on R:TS have been highly variable (Table 4). Decreases in R:TS occurred in similar percentages (13–20%) of studies conducted with agronomic, forest and natural community species; this response variable was included in only one study with horticultural species. Increases in R:TS occurred more frequently for agronomic crops, particularly root and tuber crops (Idso *et al.*, 1988), and for more of the natural community species than for forest species, which tended to have no change in R:TS under elevated CO_2. There was also large variability in R:TS response among different species within a plant-type category probably due to differing experimental conditions among studies (i.e. duration and method of exposure, interacting treatment variables, etc.).

Recently we re-examined the data previously collected by Rogers *et al.* (1983*a*) on the dry matter partitioning in soybean (C_3) and corn (C_4) exposed for 11 weeks to elevated CO_2) concentrations. Figures 8 and 9 show our results expressed as the ratios of the percent increase in the dry weight of various plant organs at three levels of elevated CO_2, in comparison with plants grown in 340 ppm 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 ppm to 718 ppm and then, increasing again at 910 ppm CO_2. An opposite pattern was observed with the stem (S) to leaf (L) ratios in both plant species. In comparison with these observations, while in soybean the root (R) to stem (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 ppm, progressively more dry matter was allocated to the stems, in comparison with 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 percent 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 ppm CO_2 (Figs 8 and 9) 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 versus 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.

Root length and number were the most frequently examined variables for horticultural species and they were examined more frequently for these species (45 and 74% of studies, respectively) compared with plants in other categories (2–12%). A majority (61–100%) of studies found that increased CO_2 resulted in more and/or longer plant roots (Table 4) which may lead to increased penetration (Baker *et al.*, 1990*a*; Rogers *et al.*, 1992*b*) and/or spread (Idso & Kimball, 1991*b*, 1992). Increasing the concentration of CO_2 in greenhouse mist systems increased the percentage of cuttings which formed roots in numerous ornamental and floricultural species (Lin & Molnar, 1981; French, 1989). Elevated CO_2 during propagation has also increased root number and length of sweet potato (Bhattacharya *et al.*, 1985*a*).

In addition to the four primary root response variables (root dry weight, root to total shoot ratio, root length and root number), many other belowground responses of plants to elevated atmospheric CO_2 have received attention (Table 4). Studies on other structural aspects of plant roots (i.e. diameter, volume, branching, relative growth rate, etc.) have usually shown positive effects of high CO_2. Tubers (number, dry weight, diameter, etc.) and nodulation (number, dry weight, activity, etc.) have also been demonstrated to benefit from elevated CO_2 in most cases.

Root function, in addition to structure, is also affected by increasing CO_2. In many species leaf turgor pressure increases and leaf water potential becomes less negative (see for example, Garbutt *et al.*, 1990) indicating an increase in water uptake by roots and/or an increase in water use efficiency. Water uptake on a whole plant basis has been shown to decline in one study with chrysanthemums (Gislerød & Nelson, 1989).

The concentration of nutrients in plant tissues is largely influenced by plant roots; as these are the primary means of extraction of nutrients for most plant species; therefore, effects of CO_2 on roots, and other belowground processes, will affect whole plant nutrition. Whole plant nutrient uptake is increased for many species under elevated CO_2 but the concentration of most nutrients on a per unit weight of tissue basis declines. 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, dilutes the concentration per unit weight. Also, nutrient utilization 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 most studies. 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

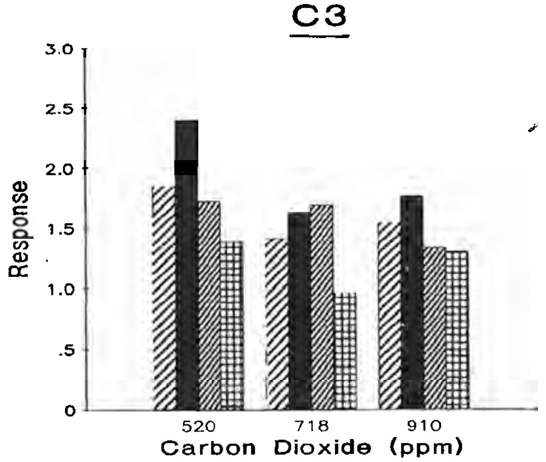


Fig 8. Ratios of percent increase in dry matter partitioning to leaves (L), stems (S), roots (R) and total shoot (TS) in the C_3 species soybean (11 weeks old) grown in open-top chambers at Raleigh, North Carolina; CO_2 concentrations were 340, 520, 718 and 910 ppm. Partitioning data were recalculated as a percentage of the dry weight of vegetative parts at 340 ppm at each elevated CO_2 level (Rogers *et al.*, 1983*a*).

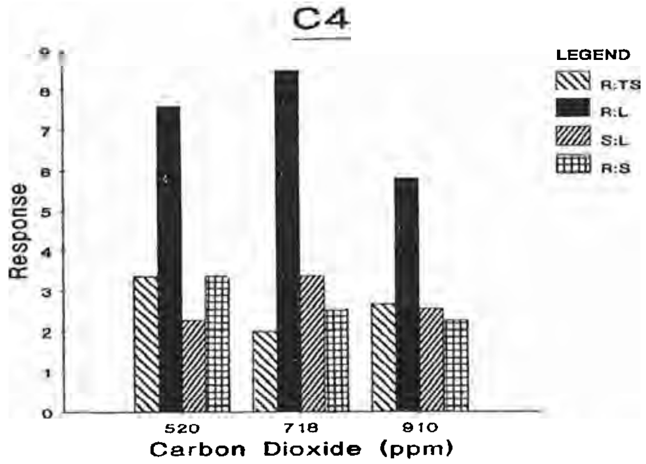


Fig 9. Ratios of percent increase in dry matter partitioning to leaves (L), stems (S), roots (R) and total shoot (TS) in the C_4 species corn (11 weeks old) grown in open-top chambers at Raleigh, North Carolina; CO_2 concentrations were 340, 520, 718 and 910 ppm. Partitioning data were recalculated as a percentage of the dry weight of vegetative parts at 340 ppm at each elevated CO_2 level (Rogers *et al.*, 1983*a*).

example, when plants are grown under nutrient levels considered adequate or poor for ambient conditions, high CO_2 results in larger plants with lower tissue nutrient concentrations (Norby *et al.*, 1986*a,b*; Yelle *et al.*, 1987), but if plants growing under higher CO_2 are supplied with higher levels of nutrients, concentration of nutrients in tissues and/or nutrient uptake efficiency are generally not significantly affected by CO_2 concentration (Israel *et al.*, 1990).

Other response variables which have been infrequently examined include parenchyma cell division and expansion, mycorrhizae and carbohydrate concentrations in roots or tubers (Table 4). These response variables, as with the others discussed, increase under elevated atmospheric CO_2. Time to harvest has also been infrequently examined but was found to decrease for root and tuber crops (Cummings & Jones, 1918).

Table 4, while not necessarily a complete compilation, does contain a predominance of the available data concerning the effects of CO_2 on roots and belowground processes. The one fact that is evident from the information in this table is that increasing levels of CO_2 in the earth's atmosphere will have virtually no adverse effects on plant root growth or function, and indeed will likely be positively affected in numerous ways which should benefit the health and productivity of most plant species.

Although Table 4 shows that many investigations on plant responses to elevated CO_2 have included effects on roots, the consideration these vital plant organs have received has been minor and often cursory; only 28% of the studies examined two or more of the four primary response variables and only 5% examined three or more of these variables. Acock and Allen (1985) in their review of 184 research reports found that, with the exception of a general increase in R:TS, there exists a serious lack of information regarding root growth response to high CO_2. The paucity of data on belowground processes has concerned several investigators and we will discuss the few, more detailed studies on crop roots and CO_2 enrichment which have recently begun to appear in the literature.

Stulen and den Hertog (1993) have recently completed a critical review of the available literature concerning effects of CO_2 on plant root growth and function. They discuss several experimental parameters which influence the response of roots to CO_2 (i.e. water, nutrients, pot size) and state that much of the variability in plant responses seen in the literature can be attributed to differential treatment of plants during the experiments, particularly in regard to R:TS. They conclude that, while more research on belowground plant growth and function is definitely required, the assumption that a larger proportion of the extra dry matter produced under CO_2 enrichment is allocated to roots needs critical reconsideration. This conclusion is supported by this review in that, while many studies have found an increase under elevated CO_2, R:TS was more variable in its response than were most of the other measurements examined (Table 4).

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 26–31% 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 contrast with those of Rogers *et al.* (1992*b*) who found a 110% increase in root length of soybean plants under high CO_2 with no change in the number of lateral roots.

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 could compensate for restriction in growth of wheat roots by drought, particularly in the upper 10 cm of soil. In contrast to finding effects of CO_2 predominating in the upper 10 cm with wheat, Chaudhuri *et al.* (1986) found that numbers and dry weights of sorghum roots were higher at all soil-profile depths (to 150 cm) under elevated CO_2.

Masle *et al.* (1990) developed a theoretical framework of the growth and carbon 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 which reduced shoot growth, reducing its sensitivity to carbohydrate substrates and thereby making more carbon 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 carbon limitation under ambient CO_2. They concluded that, if atmospheric CO_2 were not limiting, the adaptive advantage of allocating more carbon to the roots increases 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:TS increased 88–113% and that resource allocation to the root systems, measured as percent dry weight in roots, increased 75%. However, the largest increases they observed were in dry weight (173–245% increase) and in root number (130–311% increase).

The authors are currently conducting detailed research on the effects of elevated atmospheric CO_2 on roots and below ground processes in crop plants. An

Table 4. Responses of plant roots to elevated CO_2

Species	$[CO_2]$ ppm	Location	Response					Interaction	Reference
			RDW	R : TS	RL	RN	Other		
Agro-Ecosystem Components: Agriculture									
Abelmoschus esculentus	270, 350, 650	Phy	↑	—	—	—	Tissue [N]-↓	—	Overdieck *et al.* (1988)
	450, 675, 1000	Phy	↑	↑	—	—	—	—	Sionit *et al.* (1981*b*)
Arachis hypogaea	340, 1000	GC	↑	—	—	—	—	—	Chen & Sung (1990)
	Amb, 1500	GC (Field)	—	—	—	—	Nodule DW — ↑	—	Havelka & Hardy (1976)
Asparagus officinalis	330, 900, 1500	GH	↑	—	—	—	—	Light*	Desjardins *et al.* (1990)
	330, 1650, 3000	GC	—	—	—	—	Root fresh weight — ↑	Light	Laforge *et al.* (1991)
Beta vulgaris	300, 1000, 3300	GC	↑	↑	—	—	Root [sucrose] — ↑	—	Ford & Thorne (1967)
	Doubling	N/A	—	—	—	—	Root yield — ↑	—	Kimball (1983*a*)
	Doubling	N/A	—	—	—	—	Root yield — ↑	—	Kimball (1983*b*)
	350, 675	Phy	—	↑	—	—	—	Light	Sionit *et al.* (1982)
	300, 1000	GC	↑	—	—	—	Root diameter — ↑ Parenchyma cell division — ↑ Parenchyma cell expansion — ↑	O_2*	Wyse (1980)
Brassica napus	340, 680	Phy	—	↑	—	—	—	H_2O	Morison & Gifford (1984*b*)
Brassica oleracea	300, 1000, 3300	GC	—	NE	—	—	—	—	Ford & Thorne (1967)
Brassica oleracea var. *gonglyodes*	300, 900	GC	↑	—	—	—	Tuber DW — ↑ Tuber diameter — ↑ Root and tuber [N] — ↓	H_2O	Sritharan & Lenz (1990)
Citrus aurantium	Amb, +300	OTC	↑	—	—	—	—	—	Idso & Kimball (1991*a*)
	Amb +300	OTC	↑	—	—	—	Distance from tree — ↑	—	Idso & Kimball (1991*b*)
	Amb, +300	OTC	↑	—	—	—	Distance from tree — ↑	—	Idso & Kimball (1992)
Citrus paradisi × *Poncirus trifoliata*	330, 660	SPAR	↑	↓	—	—	—		Koch *et al.* (1983)
Citrus sinensis	400, 800	GC	NE	—	—	—	—	—	Downton *et al.* (1987)
Citrus sinensis × *Poncirus trifoliata*	330, 660	SPAR	↑	↓	—	—	—		Koch *et al.* (1983)
	330, 660, 990	SPAR	↑	NE	—	—	—		Koch *et al.* (1987)
Cucumis sativus	Amb, 1300	GC	↑	—	—	—	—	—	Ito (1972)
	350, 1000	Phy	↑	↑	—	—	—	—	Peet (1986)
Daucus carota var. *sativus*	340, 640	OTC	—	↑	—	—	—	—	Idso *et al.* (1988)
Echinochloa frumentacea	320, 640	GH	↑	↑	—	—	—	Light* N* Competition*	Wong & Osmond (1991)
Eleusine coracana	Amb, 800	OTC	—	—	—	—	N, P, K uptake — NE	—	Geethakumari & Shivashankar (1991)
Fragaria × *ananasa*	330, 900, 1500	GH	↑	—	—	—	Root RGR — NE	Light	Desjardinus *et al.* (1987)
Glycine max	330, 450, 600, 800	SPAR	↑	—	—	—	Root [N] — NE; Root NSC — ↑	—	Allen *et al.* (1988)
	160–990	SPAR	↑	—	—	—	—	—	Allen *et al.* (1991)
	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
	350, 1000	Phy	↑	NE	—	—	—	—	Clough & Peet (1981)
	350, 700	Phy	↑	—	—	—	—	—	Cure *et al.* (1987)
	350, 700	Phy	↑	—	—	—	N uptake efficiency — ↓ Total N — ↑, tissue [N] — ↓ N utilization efficiency — ↑	N	Cure *et al.* (1988*a*)
	350, 700	Phy	↑	—	—	—	P uptake efficiency — ↓ Total P — ↑, tissue [P] — ↓ P utilization efficiency — ↑	P*	Cure *et al.* (1988*b*)
	330, 450, 600, 800	SPAR	↑	—	↑	↑	Branching — ↑	—	Del Castillo *et al.* (1989)
	Amb, 1020	GC	↑	—	—	—	Nodule DW — ↑ Specific nodule activity — NE Total nodule activity — ↑	Exposure*	Finn & Brun (1982)

(continued)

Table 4—*contd.*

Species	[CO$_2$] ppm	Location	Response					Interaction	Reference
			RDW	R : TS	RL	RN	Other		
Glycine max (contd.)	Amb, 800	OTC	—	—	—	—	N, P, K uptake — ↑	—	Geethakumari & Shivashankar (1991)
	Amb, 1000	OTC	—	—	—	—	N_2 fixation — ↑ Specific nodule activity — ↑ Nodule fresh weight — ↑ Total N — ↑ Nitrate reductase activity — ↓	—	Hardy & Havelka (1973)
	340, 640	OTC	—	NE	—	—	—	—	Idso *et al.* (1988)
	350, 700	Phy	↑	—	—	—	Total N and P uptake — ↑ Total N and total P — NE N and P uptake efficiency — NE N and P utilization efficiency — ↑	N, P	Israel *et al.* (1990)
	330, 450, 600, 800	SPAR	↑	—	—	—	—	—	Jones *et al.* (1984)
	350, 1000	GC	—	—	—	—	Nodule DW — ↑ Total N — ↑; tissue [N] – Total nodule activity — ↑	N	Masuda *et al.* (1989)
	350, 675	Phy	—	—	—	—	Root RWR — NE	H_2O	Patterson (1986)
	350, 600, 1000	GC	—	↑	—	—	—	—	Patterson & Flint (1980)
	350, 675	Phy	—	—	—	—	Root RWR — NE	Nutrient	Patterson & Flint (1982)
	350, 675	Phy	—	—	—	—	Root RWR — ↑	Competition	Patterson *et al.* (1984)
	330, 450, 600, 800	SPAR	↑	—	—	—	—	—	Reddy *et al.* (1989*a*)
	340, 520, 720, 910	OTC	↑	—	—	—	—	—	Rogers *et al.* (1983*a*)
	350, 700	Phy	↑	↑	↑	NE	Root diameter and volume — ↑ Stele diameter and cortex Width — ↑ Root RWR and penetration — ↑ Total N — ↑ N uptake efficiency — NE	—	Rogers *et al.* (1992*b*)
	400, 1000	Phy	—	—	—	—	N uptake efficiency — ↑	Temperature*	Rufty *et al.* (1981)
	Amb, 1000	OTC	—	—	—	—	Nodule fresh weight — ↑ Specific nodule activity — ↑ Acetylene reductase activity — ↑	Straw*	Shivashankar & Vlassak (1978)
	Amb, 1000	OTC	—	—	—	—	Nodule DW and volume — ↑ Total nodule activity — ↑	—	Shivashankar *et al.* (1976)
	350, 675	Phy	↑	—	—	—	—	Nutrient	Sionit (1983)
	350, 675	Phy	—	NE	—	—	—	Light	Sionit *et al.* (1982)
	350, 675, 1000	Phy	↑	NE	—	—	—	Temperature*	Sionit *et al.* (1987)
	400, 650, 900	Phy	NE	↓	—	—	Total N — ↑; root [N] — ↑	N	Vessey *et al.* (1990)
	320, 1000	GC	↑	—	—	—	Nodule DW — ↑ Total N — ↑	N*	Williams *et al.* (1981)
Glycine soja	350, 1000	GC	↑	—	—	—	Nodule DW — ↑; total N — ↑ Total nodule activity — ↑ Leaf and stem [N] — ↓ Root and nodule [N] — ↑	N*	Masuda *et al.* (1989)
Gossypium hirsutum	340, 640	OTC	—	NE	—	—	—	—	Idso *et al.* (1988)
	Amb, 550	FACE	—	—	—	—	$\delta^{13}C$ Composition — ↑	—	Leavitt *et al.* (1993)
	340, 680	Phy	—	↑	—	—	—	H_2O	Morison & Gifford (1984*b*)
	350, 700	Phy	NE	—	—	—	Root RWR — ↓	Temperature*	Patterson *et al.* (1988)

	Amb, 550	FACE	↑		↑	—	Root volume — ↑ Root density in soil — ↑	H_2O*	Prior *et al.* (1993)
	Amb, 550	FACE	↑	↑	↑	↑	Root diameter and volume — ↑		Rogers *et al.* (1993)
	270, 350, 650	Phy	↑	—	—	—	—	Pot size*	Thomas & Strain (1991)
	330, 640	GH	—	—	—	—	Tissue [N] — ↓	—	Wong (1979)
	320, 640	GH	—	↑	—	—	Root [NSC] — ↑	N*	Wong (1990)
Helianthus annuus	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
Hordeum vulgare	300, 1000, 3300	GC	—	NE	—	—	—	Ford & Thorne (1967)	
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
Ipomoea batatas	350, 675, 1000	Phy	↑	↑	—	—	Tubers/plant — ↑; tuber DW — ↑ Tuber RGR — ↑; tuber diameter — ↑	—	Bhattacharya *et al.* (1985*a*)
	350, 675, 1000	Phy	—	—	—	—	Root [sucrose] — ↑ Root [starch and glucose] — NE Root [protein] — NE Tuber [sucrose] — ↓ Tuber [starch and glucose] — ↑ Tuber [protein] — NE	—	Bhattacharya *et al.* (1989*b*)
	364, 438, 666	OTC	↑	↑	—	—	Root fresh weight — ↑ Tuber fresh weight — ↑ Tuber [starch] — ↑	H_2O*	Bhattacharya *et al.* (1990)
	350, 675, 1000	Phy	—	—	↑	↑	—	IAA*	Bhattacharya *et al.* (1985*a*)
Lactuca sativa	380, 1200	GH	—	↓	—	—	—	NO_x*	Caporn (1989)
Lolium perenne	350, 700	GH	↑	—	—	—	—	N*,P	Goudriaan & de Ruiter (1983)
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
Lycopersicon esculentum	350, 1000	GC	↑	—	—	—		Light*	Hurd (1968)
	60–3000	GC	—	—	—	—	^{32}P uptake — ↓	Light*	Ito (1970)
	Amb, 1300	GC	↑	—	—	—	—	—	Ito (1972)
	350, 675	Phy	↑	—	—	—	Leaf H_2O potential — ↑	H_2O*	Paez *et al.* (1984)
	300, 1000	GH	↑	NE	—	—	—	Root hormone*	Tognoni *et al.* (1967)
	300, 1000	GH	↑	↑	—	—	—	—	Wittwer (1966)
	300, 1000	GH	—	↑	—	—	—	—	Wittwer (!970)
	330, 800	GH	↑	—	—	—	Total N, P, K uptake — ↑ Root [N] — ↑; leaf [N] — ↓ N, P, K uptake efficiency — NE Root N reductase activity — ↑	Root-zone temperature*	Yelle *et al.* (1987)
Macroptilium atropurpureum	340, 680	Phy	—	↑	—	—	—	H_2O	Morison & Gifford (1984*b*)
Medicago sativa	350, 700	GH	↓	—	—	—	Nodulation — ↑	N*, P	Goudriaan & de Ruiter (1983)
	350–2400	GC	↑	NE	—	—	Nodule DW — ↑ Nodule number — ↑ Nitrogenase activity — ↑	Light* NO_3* Nodulation	MacDowall (1982)
	340, 680	Phy	—	↑	—	—	—	H_2O	Morison & Gifford (1984*b*)
Olea europaea	Amb, Elev	GH	—	—	—	—	% Cuttings rooted — ↑	—	Rallo & del Rio (1990)
Oryza sativa	160–900	SPAR	↑	↑	—	—	Penetration — ↑	—	Baker *et al.* (1990*a*)
	160–3500	GC	—	—	—	—	% Dry matter in roots — ↑	—	Imai & Murata (1976)
	350, 700	GH	↑	↑	—	—	—	—	Imai *et al.* (1985)
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
Phalaris aquatica	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
Phaseolus vulgaris	340–3000	GC	NE	—	—	—	—	—	Jolliffe & Ehret (1985)
	320, 2500	GC	↑	—	—	—	—	Salinity*	Schwarz & Gale (1984)
	300, 1000	GH	↑	↑	—	—	—	Root hormone*	Tognoni *et al.* (1967)
	300, 1000	GH	↑	↑	—	—	—	—	Wittwer (1966)
	300, 1000	GH	—	↑	—	—	—	—	Wittwer (1970)

(continued)

Table 4—*contd.*

Species	[CO_2] ppm	Location	Response					Interaction	Reference
			RDW	R : TS	RL	RN	Other		
Pisum sativum	320, 1800	GC	↑	—	↑	NE	Leaf H_2O potential — ↑ Leaf tugor pressure — ↑	IAA	Davis & Potter (1982)
	Amb, Elev	?	—	—	—	—	Nodule DW — ↑ Specific N_2 fixing activity — ↑	—	Hardy & Havelka (1977)
	Amb, 1200	GC	—	—	—	—	Nodules per plant — ↑ Nodule desnity — ↑ Total N — ↑ Specific nodule activity — ↓	N	Masterson & Sherwood (1978)
	340, 680	Phy	—	NE		—	—	H_2O	Morison & Gifford (1984*b*)
	350, 1000	Phy	↑	—		—	—	—	Paez *et al.* (1980)
	350, 675	Phy	↑	—			Leaf H_2O potential — ↑	H_2O*	Paez *et al.* (1983)
	320, 120	GC	—	—		—	Nodule DW — ↑; total N — ↑ Specific nodule activity — NE	—	Phillips *et al.* (1976)
Raphanus sativus	Amb, Elev	GC	—	—	—	—	Root fresh weight — ↑ Time to harvest — ↓	—	Cummings & Jones (1918)
	340, 640	OTC	—	↑	—	—	—	—	Idso *et al.* (1988)
	Doubling	N/A	—	—	—	—	Root yield — ↑	—	Kimball (1983*a*)
	Doubling	N/A	—	—	—	—	Root yield — ↑	—	Kimball (1983*b*)
	400, 1200	GC (Field)	—	↑	—	—	Root fresh weight — ↑	—	Knecht (1975)
	340, 680	Phy	—	↑	—	—	—	H_2O	Morison & Gifford (1984*b*)
	270, 350, 650	Phy	↑	—	—	—	Tuber DW — ↑ Tissue [N] — ↓	—	Overdieck *et al.* (1988)
	350, 675	Phy	—	↑	—	—	—	Light*	Sionit *et al.* (1982)
Rubus idaeus	330, 1650, 3000	GC	↑	↑	—	↑	—	Light	Laforge *et al.* (1991)
Solanum tuberosum	Amb, Elev	GC	—	—	—	—	Tuber number — ↑ Tuber weight — ↑ Time to harvest — ↓	—	Cummings & Jones (1918)
	350, 700	GH	↓	—	—	—	Tuber DW — ↓	—	Goudriaan & de Ruiter (1983)
	350, 700	GC	↑	↑	—	—	—	Solar rad.*	Hayashi *et al.* (1990)
	Doubling	N/A	—	—	—	—	Tuber yield — ↑	—	Kimball (1983*a*)
	Doubling	N/A	—	—	—	—	Tuber yield — ↑	—	Kimball (1983*b*)
	365, 1000	GC	↑↓	—	—	—	Tuber DW — ↑	—	Wheeler & Tibbitts (1989)
	350, 1000	GC	—	—	—	—	Tuber DW — ↑	Light	Wheeler *et al.* (1991)
Sorghum bicolor	330, 485, 660, 795	GC	↑	NE	↑	↑	—	—	Chaudhuri *et al.* (1986)
	340, 680	Phy	—	↓	—	—	—	H_2O	Morison & Gifford (1984*b*)
Trifolium pratense	300–8000	GH	—	—	↑	—	Nodule number — ↑ Total N — ↑; tissue [N] — ↓	—	Wilson *et al.* (1933)
Trifolium repens	Amb, 1200	GC	—	—		—	Nodule density — NE Total N — ↑ Specific nodule activity — ↑ Root [NO_3-reductase] — NE	—	Masterson & Sherwood (1978)
	340, 680	Phy	—	↑	—	—	—	H_2O	Morison & Gifford (1984*b*)
	200, 350, 1000	GC	↑	↑	—	—	Root [NSC] — ↑	—	Scheidegger & Nösberger (1984)
Triticum aestivum	340, 485, 660, 825	GC (Field)	↑	NE	—	—	Penetration speed — ↑	H_2O	Chaudhuri *et al.* (1990)
	330, 660	GC	↑	—	—	—	Dry matter partitioning — NE	Density*	Du Cloux *et al.* (1987)
	–150, Amb, +200	Phy	—	—	—	—	% Dry weight in roots — NE	Light	Gifford (1977)

	Amb, +250	Phy	↑	↓	—	—	—	H_2O*	Gifford (1979)
	350, 700	GH	↑	—	—	—	—	N*, P	Goudriaan & de Ruiter (1983)
	Amb, 1500	GH	↑	↑	—	—	% Dry matter in roots — ↑ Total N — ↑ N use efficiency — ↑ Nitrate reductase activity — ↓	N*	Hocking & Meyer (1991)
	350, 700	GC	↑	↓	—	—	Root [^{14}C] — NE	—	Lekkerkerk *et al.* (1990)
	350, 1300, 2200	GH	↑	↑	—	—	—	Light*	MacDowall (1972)
	120, 220, 320, 500	GC	↑	↓	—	—	Root [carbohydrates] — ↑	Compaction*	Masle *et al.* (1990)
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
	350, 1000	Phy	↑	NE	—	—	—	H_2O*	Sionit *et al.* (1980)
	350, 675	Phy	↑	↑	—	—	—	Nutrient*	Sionit *et al.* (1981*a*)
	350, 675, 1000	Phy	—	↑	—	—	—	—	Sionit *et al.* (1981*c*)
	350, 1000	Phy	↑	NE	—	—	—	H_2O	Sionit *et al.* (1981*d*)
	320, 640	GH	↑	↑↓	—	— —	—	Light*, N* Competition*	Wong & Osmond (1991)
Vicia faba	330, 350, 700	GH	↑	—	—	—	Nodulation — ↑	N*, P	Goudriaan & de Ruiter (1983)
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
Vigna unguiculata	350, 675, 1000	Phy	↑	—	—	—	—	—	Bhattacharya *et al.* (1985*b*)
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
	270, 350, 650	Phy	↑	—	—	—	Leaf and stem [N] — ↓ Root [N] — ↑	—	Overdieck *et al.* (1988)
Vitus vinifera	Amb, 1200	GC	↑	↑	—	—	—	—	Kriedemann *et al.* (1976)
Zea mays	300, 600, 1200	GC in GH	NE	—	—	—	—	—	Carlson & Bazzaz (1980)
	350, 700	GH	↑	—	—	—	—	N*, P	Goudriaan & de Ruiter (1983)
	Amb, 1500	GH	NE	—	—	—	Total N and root [N] — NE N use efficiency — NE Nitrate reductase activity — NE	N	Hocking & Meyer (1991)
	160–3500	GC	—	—	—	—	Dry matter partitioning — NE	—	Imai & Murata (1976)
	350, 600, 800	GC	NE	—	—	—	—	H_2O	King & Greer (1986)
	340, 680	Phy	—	NE	—	—	—	H_2O	Morison & Gifford (1984*b*)
	350, 600, 1000	GC	—	NE	—	—	—	—	Patterson & Flint (1980)
	340, 520, 720, 910	OTC	↑	—	—	—	—	—	Rogers *et al.* (1983*a*)
	320, 2500	GC	NE	—	—	—	—	Salinity	Schwarz & Gale (1984)
	350, 675	Phy	—	NE	—	—	—	Light	Sionit *et al.* (1982)
	400, 550, 800	GC	↑	↑	—	—	Root RGR — ↑	—	Whipps (1985)
	330, 640	GH	—	—	—	—	Tissue [N] — NE	—	Wong (1979)
Agro-Ecosystem Components: Horticulture									
Begonia argenteo-guttata	350, 1200	GC	↑	—	↑	NE	—		Davis & Potter (1983)
Callistephus chinensis	325, 600, 900	GC	↑	—	—	—	—	—	Hughes & Cockshull (1969)
Camellia japonica	Amb, 1100 (Mist)	GH	—	—	—	↑	—	Season*	French & Alsbury (1989)
Campanula isophylla	300, 900, 1800	GC	—	—	↑	↑	—	Light* Temperature	Moe (1977)
Chamaecyparis sp.	300, 1050 (Mist)	GH	—	—	—	—	% Cuttings rooted — ↑	—	Lin & Molnar (1980)
Chrysanthemum sp.	Amb, 1900	GC	↑	—	—	↑	% Cuttings rooted — ↑		Molnar & Cummings (1968)
	300, 1650 (Mist)	GH	—	—	—	↑	% Cuttings rooted — NE	—	Molnar & Cummings (1968)
Chrysanthemum morifolium	340, 940	GC	↑	↓	—	—	H_2O uptake/cm^2 leaf — NE Total H_2O uptake — ↓	RH*	Gislerød & Nelson (1989)
Ficus pumila	350, 1200	GC	—	—	NE	NE	—	—	Davis & Potter (1983)
Fuchsia magellanica	350, 1200	GC	↑	—	↑	NE	—	—	Davis & Potter (1983)
Hemigraphis alternata	350, 1200	GC	—	—	↑	NE	—	—	Davis & Potter (1983)

(*continued*)

Table 4—*contd.*

Species	[CO$_2$] ppm	Location	Response RDW	R : TS	RL	RN	Other	Interaction	Reference
Ilex aquifolium	300, 1050 (Mist)	GH	—	—	—	—	% Cuttings rooted — ↑ Rootball diameter — ↑	Light	Lin & Molnar (1981)
Ilex crenata	300, 1050 (Mist)	GH	—	—	—	—	% Cuttings rooted — NE	Light	Lin & Molnar (1980)
Impatiens balsamina	350, 675, 1000	Phy	—	—	—	↑	—	IAA*	Bhattacharya *et al.* (1989*a*)
Juniperus horizontalis	300, 1650 (Mist)	GH	—	—	—	↑	% Cuttings rooted — ↑	—	Molnar & Cummings (1968)
Juniperus sabina	300, 1050 (Mist)	GH	—	—	↑	↑	% Cuttings rooted — NE	Light	Lin & Molnar (1981)
Juniperus squamata	300, 1050 (Mist)	GH	—	—	NE	NE	% Cuttings rooted — NE	Light	Lin & Molnar (1981)
Magnolia sieboldii	300, 1050 (Mist)	GH	—	—	↑	NE	% Cuttings rooted — NE	Light	Lin & Molnar (1981)
Magnolia soulangiana	300, 1050 (Mist)	GH	—	—	↑	↑	% Cuttings rooted — ↑	Light*	Lin & Molnar (1981)
Osmanthus heterophyllus	350, 1200	GC	NE	—	NE	NE	—	—	Davis & Potter (1983)
Pelargonium × *hortorum*	350, 1200	GC	—	—	NE	NE	—	—	Davis & Potter (1983)
Peperomia glabella	350, 1200	GC	↑	—	↑	↑	—	—	Davis & Potter (1983)
Peperomia nivalis	350, 1200	GC	↑	—	↑	NE	—		Davis & Potter (1983)
Potentilla fruticosa	Amb, 1900	GC	—	—	—	↑	% Cuttings rooted — ↑	—	Molnar & Cummings (1968)
	300, 1650	GH	—	—	—	↑	% Cuttings rooted — NE	—	Molnar & Cummings (1968)
Rhododendron sp.	Amb, 1100 (Mist)	GH	—	—	—	—	% Cuttings rooted — ↑	Season*	French (1989)
	300, 1050 (Mist)	GH	—	—	—	—	% Cuttings rooted — ↑ Rootball diameter — ↑	Light*	Lin & Molnar (1981)
Rosa hybrida	300, 1000, 2000	GH	—	—	—	—	Root systems smaller at 2000	—	Mattson & Widmer (1971)
Taxus × *media*	300, 1050 (Mist)	GH	—	—	↑	↑	Root fresh weight — ↑	—	Lin & Molnar (1980)
Thuja occidentalis	300, 1650 (Mist)	GH	—	—	—	↑	% Cuttings rooted — ↑	—	Molnar & Cummings (1968)
Weigela sp.	Amb, 1900	GC	—	—	—	↑	% Cuttings rooted — ↑	—	Molnar & Cummings (1968)
Forest Ecosystem Components									
Acer rubrum	400, 700	GC	—	NE	—	—	—	—	Bazzaz *et al.* (1990)
Acer saccharinum	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
Acer saccharum	400, 700	GC	—	NE	—	—	—	—	Bazzaz *et al.* (1990)
Alnus glutinosa	350, 700	GC	—	—	—	—	RWR — NE; nodule DW — ↑ Nodule weight ratio — ↑ Total nodule activity — ↑ Specific nodule activity — NE Total N, P, K, Ca — NE; total Mg — ↑ [N], [P], [K], [Ca] — ↓; [Mg] — NE	—	Norby (1987)
Alnus rubra	350, 650	GC	↑	—	—	—	Nodules/plant — NE Nodule DW — NE Tissue [N] — ↑ Specific nitrogenase activity — ↑ Total nitrogenase activity — ↑	N* Nodulation*	Arnone & Gordon (1990)
Betula sp.	300, 1000, 2000	GH	—	—	↑	—	—		Hårdh (1966)
Betula papyrifera	400, 700	GC	—	NE	—	—	—	—	Bazzaz *et al.* (1990)
Castanea sativa	350, 700	GC	↑	↑	—	—	—	—	Mousseau & Enoch (1989)
Cedrus atlanticus	350, 800	GH	↑	NE	↑	↑	Root [starch] — NE	—	Kaushal *et al.* (1989)
Elaeagnus angustifolia	350, 700	GC	—	—	—	—	RWR —↓; nodule DW — NE Nodule weight ratio — NE Total nodule activity — NE Specific nodule activity — NE	—	Norby (1987)

							Total N, P, K, Ca, Mg — NE [N], [P], [K], [Ca] — ↓; [Mg] — NE		
Fagus grandifolia	400, 700	GC	—	↓	—	—	—	—	Bazzaz *et al.* (1990)
Liquidambar styraciflua	340, 520, 720, 910	OTC	↑	—	—	—		—	Rogers *et al.* (1983*a*)
	350, 500, 650	Phy	↑	↓	—	—	—	—	Sionit *et al.* (1985)
	350, 675, 1000	Phy	—	↓	—	—		H_2O*	Tolley & Strain (1984*a*)
	350, 675, 1000	Phy	—	↓	—	—	—	Light	Tolley & Strain (1984*b*)
Liriodendron tulipifera	367, 692	GC	↑	↑	—	—	Total N & Mn — NE Total P, K, other nutrients — ↑ [K], other nutrients — NE [N], [P], other nutrients — ↓	—	O'Neill *et al.* (1987*a*)
	Amb, + 150, + 300	OTC	↑	NE	—	—	—	—	Norby *et al.* (1992)
Ochroma lagopus	350, 675	Phy	—	NE	—	—		—	Oberbauer *et al.* (1985)
Pentaclethra macroloba	350, 675	Phy	—	NE	—	—		—	Oberbauer *et al.* (1985)
Picea sp.	300, 1000, 2000	GH	—	—	↑	—	—	—	Hårdh (1966)
Picea glauca	350, 750	GC	↑	—	—	—	RWR — ↑	N*	Brown & Higginbotham (1986)
	330, 600, 1000	GC	↑	—	—	—	—	—	Higginbotham (1983)
Picea mariana	340, 1000	GC in GH	↑	↑	—	—	Root RGR — ↑ Root NSC — NE	—	Campagna & Margolis (1989)
Picea pungens	325, 1200	GC in GH	↑	NE	—	—	Root fresh weight — ↑	—	Tinus (1972)
Pinus sp.	300, 1000, 2000	GH	—	—	↑	—	—	—	Hårdh (1966)
Pinus contorta	330, 1000, 2000	GC	↑	—	—	—	—	—	Higginbotham *et al.* (1985)
Pinus echinata	368, 695	GC	↑	—	—	—	%^{14}C in roots — ↑ Mycorrhizal density — ↑	—	Norby *et al.* (1987)
	360, 700	GC	↑	NE	↑↓	—	Mycorrhizae — NE	Mycorrhizae*	O'Neill *et al.* (1987*b*)
Pinus nigra	350, 800	GH	NE	NE	—	—	Root [starch] — NE	—	Kaushal *et al.* (1989)
Pinus ponderosa	325, 1200	GC in GH	↑	NE	—	—	Root fresh weight — ↑	—	Tinus (1972)
Pinus strobus	400, 700	GC	—	NE	—	—	—	—	Bazzaz *et al.* (1990)
Pinus taeda	340, 520, 720, 910	OTC	↑	—	—	—	—	—	Rogers *et al.* (1983*a*)
	350, 500 650	Phy	↑	NE	—	—	—		Sionit *et al.* (1985)
	350, 675, 1000	Phy	—	NE	—	—	—	H_2O	Tolley & Strain (1984*a*)
	350, 675, 1000	Phy	—	↑↓	—	—	—	Light*	Tolley & Strain (1984*b*)
Pinus virginiana	340–940	OTC	↑	↑	—	—	Nutrient uptake — ↑	—	Luxmoore *et al.* (1986)
Platanus occidentalis	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
Populus deltoides	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
Populus euramericana	350, 700	GH	↑	—	—	—	—	N*, P*	Goudriaan & de Ruiter (1983)
Populus tremuloides	350, 750	GC	↑	—	—	—	RWR — NE	N*	Brown & Higginbotham (1986)
Prunus serotina	400, 700	GC	—	NE	—	—	—	—	Bazzaz *et al.* (1990)
Pseudotsuga menziesii	300, 1050 (Mist)	GH	—	—	↑	↑	Root fresh weight — ↑	—	Lin & Molnar (1980)
	300, 1000, 10000	GC	—	—	—	↑	Roots shorter and more branched	—	Purohit & Tregunna (1976)
Quercus alba	389, 496, 793	GC	↑	—	—	—	—	N, P*	Norby & O'Neill (1989)
	363, 690	GC	↑	↑	—	—	Total N — NE; total P, K — ↑ N uptake efficiency — ↓ P and K uptake efficiency — NE Tissue [N] — ↓ Mycorrhizae — NE	—	Norby *et al.* (1986*a*)
	362, 690	GC	↑	↑	—	—	Total N — NE; total P, K — ↑ N uptake efficiency — ↓ N use efficiency — ↑ P and K uptake efficiency — NE Tissue [N] — ↓	—	Norby *et al.* (1986*b*)
	360, 700	GC	↑	NE	—	—	Mycorrhizae — ↑	—	O'Neill *et al.* (1987*b*)

(*continued*)

Table 4—*contd.*

Species	$[CO_2]$ ppm	Location	Response					Interaction	Reference
			RDW	R : TS	RL	RN	Other		
Robinia pseudoacacia	350, 700	GC	—	—	—	—	RWR — NE; nodule DW — ↑ Nodule weight ratio — NE Total nodule activity — ↑ Specific nodule activity — NE Total N, P, K, Ca, Mg — NE [N] — ↓; [P], [K], [Ca], [Mg] — NE	—	Norby (1987)
Tsuga canadensis	400, 700	GC	—	NE	—	—	—	—	Bazzaz *et al.* (1990)
Natural Community Components									
Abutilon theophrasti	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
	350, 700	GC in GH	—	—	—	—	Leaf H_2O potential — ↑ Leaf [N] — ↓	—	Garbutt *et al.* (1990)
	350, 600, 1000	GC	—	↑	—	—	—	—	Patterson & Flint (1980)
	350, 700	Phy	↑	—	—	—	RWR — NE	Temperature*	Patterson *et al.* (1988)
Agropyron smithii	340, 680	GH	—	NE	—	—		—	Smith *et al.* (1987)
Amaranthus edulis	340, 680	Phy	—	↓	—	—	—	H_2O	Morison & Gifford (1984*b*)
Amaranthus retroflexus	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
	300, 600, 1200	GC in GH	—	↑	—	—	—	SO_2*	Carlson & Bazzaz (1982)
	350, 700	GC in GH	—	—	—	—	Leaf H_2O potential — ↑ Leaf [N] — ↓	—	Garbutt *et al.* (1990)
Ambrosia artemisiifolia	300, 600, 1200	GC in GH	↑	—	—	—	—	—	Carlson & Bazzaz (1980)
	350, 700	GC in GH	—	—	—	—	Leaf H_2O potential — ↑ Leaf [N] — ↓	—	Garbutt *et al.* (1990)
Andropogon gerardii	350, 700	OTC	—	—	—	—	Total N and P — ↑ Root N and P — ↑ Aboveground [N] — ↓; [P] — NE Root [N] — NE; [P] — ↓	—	Owensby *et al.* (1993*a*)
	350, 700	OTC	↑	—	—	—		—	Owensby *et al.* (1993*b*)
Andropogon glomeratus	350, 500, 650	Phy	↓	NE	—	—	—	Salinity*	Bowman & Strain (1987)
Anoda cristata	350, 700	Phy	NE	—	—	—	RWR — NE	Temperature	Patterson *et al.* (1988)
Artemisia tridentata	350, 650	Phy	NE	↑	—	—	Leaf [NE] — ↓	Nutrient*	Johnson & Lincoln (1991)
Atriplex halimus	320, 2500	GC	↑	—	—	—	—	Salinity*	Schwartz & Gale (1984)
Betula nana	350, 675	Phy	NE	NE	—	—	Leaf [N], [P], [K], [Ca], [Mg] — ↓ Other leaf [nutrients] — NE	Nutrient	Oberbauer *et al.* (1986)
Bouteloua gracilis	350, 675, 1000	Phy	NE	—	—	—	—	—	Riechers & Strain (1988)
Bromus mollis	350, 650	Phy	↑	↑	—	—	Leaf [N] — ↓	N*	Larigauderie *et al.* (1988)
Bromus tectorum	340, 680	GH	—	NE	—	—	—	—	Smith *et al.* (1987)
Carex bigelowii	350, 675	Phy	NE	↑	—	—	Leaf [N, [P], [K], [others] — ↑	Nutrient*	Oberbauer *et al.* (1986)
Cassia obtusifolia	350, 675	Phy	—	—	—	—	RWR — NE	Nutrient	Patterson & Flint (1982)
Chenopodium album	300, 600, 1200	GC in GH	—	NE	—	—	—	SO_2*	Carlson & Bazzaz (1982)
	350, 700	GC in GH	—	—	—	—	Leaf H_2O potential ↑ Leaf [N] — ↓	—	Garbutt *et al.* (1990)
Crotalaria spectabilis	350, 675	Phy	—	—	—	—	RWR — ↓	Nutrient*	Patterson & Flint (1982)
Datura stramonium	300, 600, 1200	GC in GH	↑	—	—	—		—	Carlson & Bazzaz (1980)
	300, 600, 1200	GC in GH	—	NE	—	—		SO_2*	Carlson & Bazzaz (1982)
Desmodium paniculatum	350, 1000	Phy	—	NE	—	—	—	—	Wulff & Strain (1982)
Digitaria ciliaris	350, 675	Phy	—	—	—	—	RWR — ↑	H_2O*	Patterson (1986)

Echinochloa crus-galli	350, 675	Phy	—	—	—	—	RWR — NE	H_2O*	Patterson (1986)
	350, 675	Phy	↑	—	—	—	—	Temperature*	Potvin & Strain (1985)
Eleusine indica	350, 675	Phy	—	—	—	—	RWR — ↓	H_2O*	Patterson (1986)
	350, 675	Phy	↑	—	—	—	—	Temperature*	Potvin & Strain (1985)
Eragrostis orcuttiana	340, 680	GH	—	NE	—	—	—	—	Smith *et al.* (1987)
Festuca arundinacea	330, 660	GC	—	—	—	—	N uptake — NE	—	Gastal & Saugier (1989)
Festuca elatior	350, 600	GC in GH	↑	↑	—	—	RWR — ↑	Competition*	Carter & Peterson (1983)
Layia platyglossa	300–2100	GC	—	—	—	—	Root stele diameter — NE Root tracheary element wall thickness and diameter — NE	—	St. Omer & Horvath (1984)
Ledum palustre	350, 675	Phy	NE	↑	—	—	[N], [P], [K], [Ca], [Mg] — NE	—	Oberbauer *et al.* (1986)
Lonicera japonica	350, 675, 1000	Phy	↑	—	—	—	—	—	Sasek & Strain (1990)
Nymphaea sp.	350, 650	OTC	↑	—	—	↑	Number of new rhizomes — ↑	—	Idso *et al.* (1990)
Oryzopsis hymenoides	340, 680	GH	—	↑	—	—	—	—	Smith *et al.* (1987)
Plantago lanceolata	380, 700	GC	↑	↑	—	—	—	Herbivory	Fajer *et al.* (1991)
Plantago major	350, 700	GC	—	↓	—	—	Root [starch] — NE Root respiration — ↑	—	Poorter *et al.* (1988)
Poa pratensis	350, 700	OTC	—	—	—	—	Aboveground N — ↓; [N] — ↓ Root N — ↑; Root [N] — NE Aboveground [P] — NE; [P] — ↓ Root P — ↑; root [P] — ↓	—	Owensby *et al.* (1993*a*)
	350, 700	OTC	↑	—	—	—	—	—	Owensby *et al.* (1993*b*)
Polygonum pensylavanicum	300, 600, 1200	GC in GH	—	NE	—	—	—	SO_2*	Carlson & Bazzaz (1982)
Pueraria lobata	350, 675, 1000	Phy	↑	↓	↑	—	RWR — ↓	—	Sasek & Strain (1988)
	350, 675, 1000	Phy	↑	—	—	—	—	—	Sasek & Strain (1990)
Rottboellia exaltata	350, 600, 1000	GC	—	NE	—	—	—	—	Patterson & Flint (1980)
Scirpus olneyi	Amb, +338	OTC	↑	—	—	—	Root [N] — ↓ Rhizome DW — ↑	Competition*	Curtis *et al.* (1990)
Setaria faberii	300, 600, 1200	GC in GH	—	↓	—	—	—	SO_2*	Carlson & Bazzaz (1982)
	350, 700	GC in GH	—	—	—	— —	Leaf H_2O potential — ↑ Leaf [N] — ↓	—	Garbutt *et al.* (1990)
Setaria lutescans	300, 600, 1200	GC in GH	—	↓	—	—	—	SO_2*	Carlson & Bazzaz (1982)
Sorghum halepense	350, 600	GC in GH	↑	↑	—	—	RWR — ↑	Competition*	Carter & Peterson (1983)
	350, 675	Phy	—	—	—	—	RWR — ↑	Competition*	Patterson *et al.* (1984)
Spartina alterniflora	100, 900	GC (field)	—	—	—	—	Total and root acetylene Reductase activity — ↑	—	Whiting *et al.* (1986)
Spartina patens	Amb, +338	OTC	NE	—	—	—	Root [N] — NE Rhizome DW — NE	Competition	Curtis *et al.* (1990)
Xanthium occidentale	Amb, 1500	GH	↑	NE	—	—	Root [N] — ↑	N*	Hocking & Meyer (1985)
Xanthium strumarium	320, 2500	GC	↑	—	—	—	—	Salinity*	Schwarz & Gale (1984)

Concentrations are in ppm CO_2. Amb = ambient (+ or – refers to ppm CO_2 above or below ambient). Elev = elevated.
Locations: GC = growth chamber; GH = glasshouse (including plastic houses); N/A = not applicable (for reviews; Kimball, 1983*a,b*); OTC = open top chamber; SPAR = sunlit plant–atmosphere research chamber; Phy = phytotron ; FACE = free-air CO_2 enrichment system.
Responses: RDW = root dry weight; R : TS = total root to total shoot ratio (usually on dry weight basis); RL = root length; RN = root number; ↑ = increase; ↓ = decrease; NE = no effect.
Definitions of terms used: total = per plant; specific = per unit weight of tissue; uptake efficiency = unit of nutrient per unit weight of root; utilization efficiency = unit of biomass produced per unit of nutrient; DW = dry weight; NSC = nonstructural carbohydrates; [ ] = amount per unit weight of tissue; RGR = relative growth rate (growth per unit time); RWR = root weight ratio (ratio weight/whole plant weight).
Interactions indicates variables which were examined. An asterisk (*) indicates the interaction of the variable with CO_2 concentration was significant.

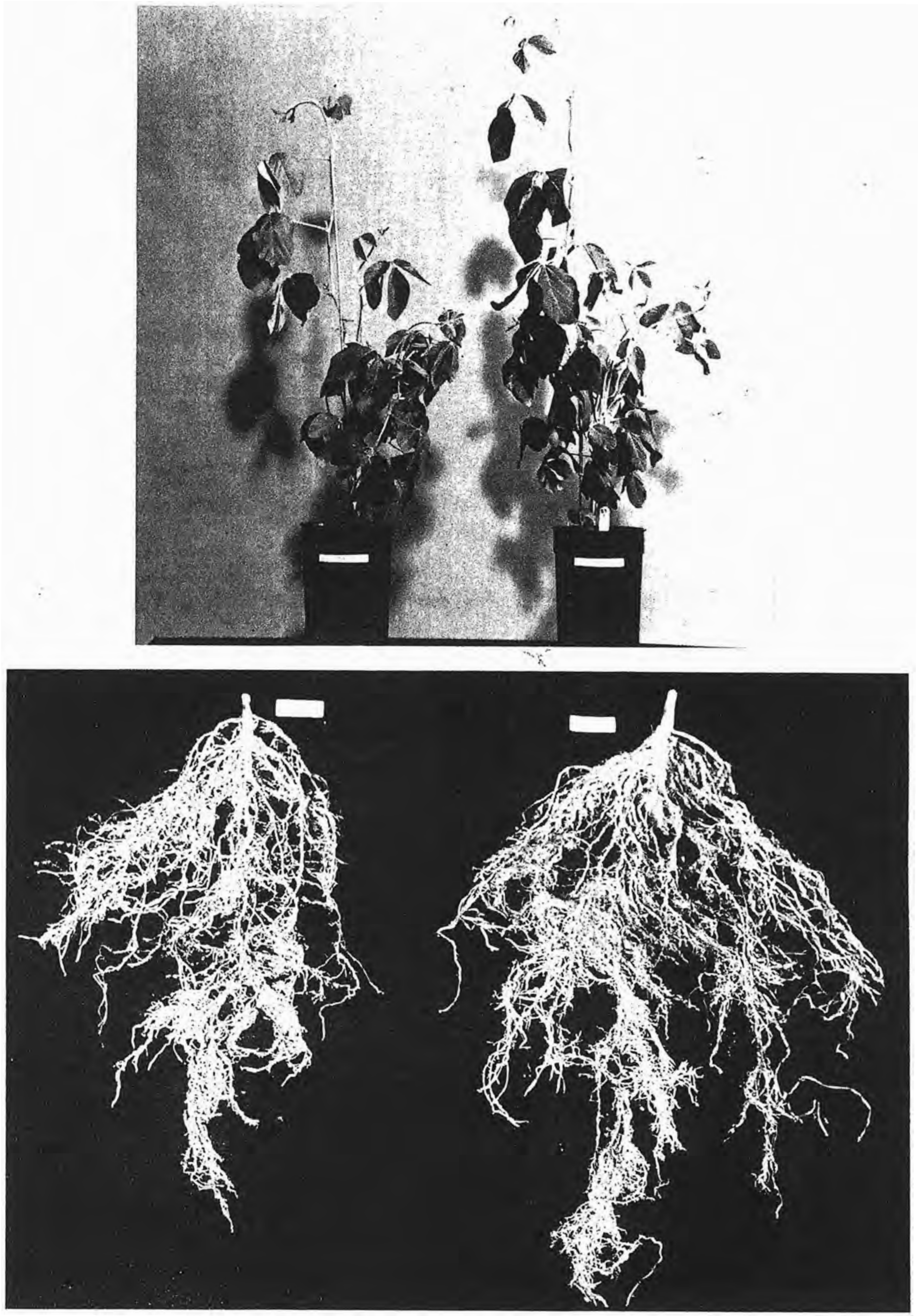
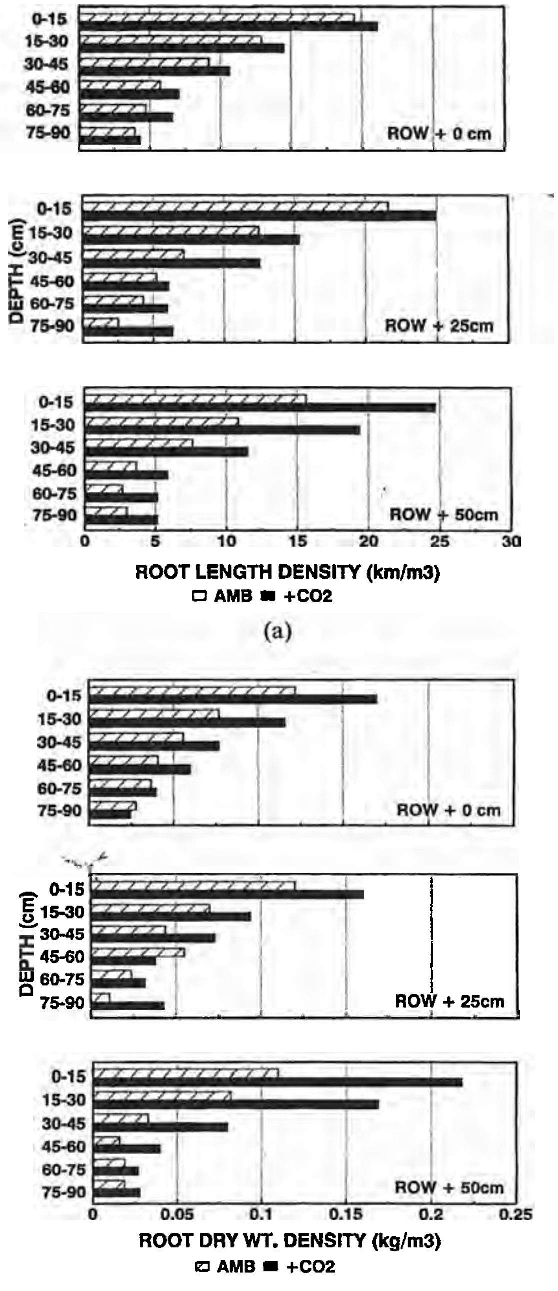


Fig. 10. Photographs of 35 day old soybean plants and their root systems grown at 350 ppm (left) and 700 ppm CO_2 (right) in growth rooms of the Duke University Phytotron.

example of this research can be seen in Fig. 10, where the soybean plant grown with air containing a twice ambient concentration of CO_2 has a visually larger root system than the one grown in ambient air. Rogers *et al.* (1992*b*) demonstrated significant increases in root dry weight, volume, diameter, R:TS weight ratio, as well as root length at most soil depths to 50 cm, for high CO_2-grown soybean plants. However, the total number of soybean roots (and numbers of roots) at most depths exhibited no response to CO_2 enrichment.

Laboratory work has also been conducted on cotton plants in connection with the FACE project (Prior, 1992, Prior *et al.*, 1993; Rogers *et al.*, 1993). Dry weights, lengths and volumes of taproots, lateral roots and fine roots tended to be higher for CO_2 enriched cotton plants, even when CO_2 exposures occurred for only six weeks. 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 tended to provide 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 (Figs 11a and b). The density of fine roots was seen to increase under CO_2 enrichment at most depths to 90 cm, but was increased more significantly in the upper 45 cm of the soil profile. 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 under elevated CO_2. Research efforts concerning the effects of CO_2 on belowground processes are continuing in our laboratory, where we are currently investigating effects of elevated CO_2 on interacting aspects of root growth, root exudation, carbon cycling in soil, mineral weathering, and soil microbiology in a C_3 (soybean) and a C_4 (sorghum) crop.

Detailed work with roots and belowground responses of crops plants to atmospheric CO_2 enrichment have added substantial support to the findings of the more numerous cursory reports in that increasing concentrations of CO_2 result in, often dramatic, increased root growth parameters. Detailed research is also being conducted with non-agronomic crop plants. 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.*



(a)

(b)

Fig. 11. (a) Root length density and (b) root dry weight density of cotton eight weeks after planting during vegetative growth under ambient level CO_2 (360 ppm) and free-air CO_2 enrichment (550 ppm) in Maricopa, Arizona (Prior, 1992).

Substantial CO_2 research has been conducted at Oak Ridge National Laboratory with several forest tree species, including shortleaf pine (Norby *et al.*, 1987; O'Neill *et al.*, 1987*b*), Virginia pine (Luxmoore *et al.*, 1986), white oak (Norby *et al.*, 1986*a,b*; O'Neill *et al.*, 1987*b*; Norby & O'Neill, 1989), yellow poplar (O'Neill *et al.*, 1987*a*; Norby *et al.*, 1992), and nitrogen-fixing woody plants (Norby, 1987). Generally, these tree species have demonstrated increases in root dry weight, R:TS, nutrient uptake, carbon 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 (Kaushal *et al.*, 1989), demonstrated positive but varying root responses to CO_2 enrichment which the authors related to differences in phenological root growth patterns between the two species.

Research with natural community plant species has demonstrated increased root dry mass for *Scirpus*, but not for *Spartina*, at depths up to 15 cm, while roots of mixed communities of the two species were significantly different only at the 10–15 cm depth (Curtis *et al.*, 1990). *Scripus*, whether alone or in mixed communities, also demonstrated lower percent nitrogen and, thus, higher C:N ratios when grown under elevated CO_2. Recent detailed studies in a tallgrass prairie ecosystem (Owensby *et al.*, 1993*b*) have demonstrated increased root biomass production for some species which may have led, at least in part, to alterations in species composition. Other work in this ecosystem (Owensby *et al.*, 1993*a*) with nutrient dynamics demonstrated that total and/or root nitrogen and phosphorus contents tended to increase, while concentrations on a per unit weight of tissue basis tended to be lower under CO_2 enrichment.

Even though more and detailed studies are being conducted on the effects of elevated atmospheric CO_2 on belowground plant structure and function, this area of research remains largely neglected. Progress toward understanding subterranean processes has often been hampered by a lack of effective methodology with which to study plant roots and soil dwelling organisms. New and better approaches to the study of roots and the rhizosphere are indeed needed and are beginning to be developed, including new extraction techniques (Prior & Rogers, 1992), minirhizotrons (Kaushal *et al.*, 1989), NMR imaging (Bottomley *et al.*, 1993), and $\delta^{13}C$ determinations of belowground carbon allocation (Wong & Osmond, 1991; Leavitt *et al.*, 1993).

RHIZOSPHERE

Increasing levels of atmospheric CO_2 will influence not only plant roots but also the environment of those roots. The rhizosphere, defined by Curl and Truelove (1986) as 'that narrow zone of soil subject to the influence of living roots', is not likely to be directly influenced by increasing atmospheric CO_2 since its concentration in the soil is already ten to fifty times that existing in the atmosphere (Lamborg *et al.*, 1983). However, plant mediated responses to elevated CO_2 in the atmosphere have the potential to alter the deposition of materials by plant roots into the rhizosphere and, thus, rhizosphere microbial composition and activity. These impacts on the rhizosphere will greatly affect the health and productivity of plants growing in future, higher CO_2 environments.

An important connection between the rhizosphere and root systems of some crop plants, the legumes, is nitrogen fixation (the incorporation of atmospheric nitrogen into nitrogenous compounds which can be utilized by living organisms). Legume/bacterial symbiosis is significantly increased by elevated CO_2 levels (Reddy *et al.*, 1989*a*; Reardon *et al.*, 1990). Phillips *et al.* (1976) obtained results indicating that short-term high CO_2 exposures increased fixation by affecting nodule function in peas while long-term enrichment promoted fixation by enhancing nodule development. In their work with white clover, Masterson and Sherwood (1978) found that the normally expected reduction in nitrogen fixation at high levels of nitrogen did not occur at elevated CO_2 concentrations. Acock (1990) concluded that, in general, the increase appears to be mainly due to larger biomass, i.e. bigger plants, more carbon allocation for nitrogen fixation.

Mycorrhizae, the symbiotic association of plant roots with fungi, represent another intimate interface between roots and rhizosphere microorganisms. It has been hypothesized that elevated atmospheric CO_2 will result in increased mycorrhizal colonization of plant roots (Luxmoore, 1981; Lamborg *et al.*, 1983), which in turn will increase plant productivity. Mycorrhizae increase nutrient uptake by their host plants (Abbott & Robson, 1984) and may even increase nutrient availability in some soils (Graustein *et al.*, 1977). Mycorrhizae can also provide additional water to plants through hyphal proliferation in soil (Luxmoore, 1981) which may, at least in part, explain the observed increase in biomass of CO_2-enriched plants under drought stress. Mycorrhizae will affect plant health by protecting roots from pathogenic microorganisms (Marx, 1973). Carbon dioxide enrichment has increased mycorrhizal colonization of roots of shortleaf pine (Norby *et al.*, 1987; O'Neill *et al.*, 1987*b*) and white oak (O'Neill *et al.*, 1987*b*).

The effects of CO_2 on nitrogen-fixing bacteria and mycorrhizal fungi are mediated through plants, primarily by altering rhizodeposition (the release of cells, exudates, mucilages, and other compounds into the rhizosphere by plant roots). In a historical review on the subject, Börner (1960) stated it has been known for some time that roots exude materials into the rhizosphere. There have recently been several excellent reviews on this topic (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 carbon fluxes in plant–soil systems and speculated that increased plant biomass production under high CO_2 may lead to increased carbon inputs and increased microbial activity in the rhizosphere. Whipps (1985) found that the percentage of root-translocated carbon released from maize roots was not significantly affected by CO_2 concentration. However, Norby *et al* (1987) found that exudation of soluble, ^{14}C-labeled compounds from shortleaf pine seedling roots was greater in plants growing in CO_2-enriched air for up to 34 weeks. Finally, Lekkerkerk *et al* (1990) reported increases in carbon transported to all parts of the plant-soil system, including carbon lost through root exudation and soil/root respiration, proportional to the increase in photosynthetic fixation of carbon 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. Effects of elevated CO_2 on rhizosphere deposition may have important implications to the development of rhizosphere biota (Curl & Harper, 1990; Lynch, 1990) including disease suppression (Curl, 1988). However, little attention has been paid to this aspect of plant development.

Effects of CO_2 on rhizodeposition will drive changes in root-soil microbial composition and activity which will affect not only nitrogen-fixing bacteria and mycorrhizal fungi but also pathogenic and nutrient cycling microbes. Changes in the concentration of CO_2 in the soil are known to affect soil microorganisms (Gardner & Hendrix, 1973; Ioannou *et al.*, 1977), but data on the effects of elevated atmospheric CO_2 on soil-borne pathogens and on root diseases are virtually non-existent. 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.* (1993) observed a trend toward decreasing numbers of parasitic nematodes in root-zone soil of cotton plants grown under high CO_2. They also reported a trend for increased populations of *Rhizoctonia solani*, a cotton root pathogen, but observed no corresponding increase in cotton root disease in a bioassay using root-zone soil from high CO_2 grown plants.

Microbes are responsible for the cycling of nutrients in soils and impacts of increasing CO_2, both on biomass production and on microbial composition and activity, will affect cycling processes. 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.* (1987*a*) found an increase in total nitrogen and phosphorus 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. Dehydrogenase activity, a measure of microbial respiration, was significantly higher in soils from CO_2-enriched cotton plants, but no appreciable differences in microbial populations (fungi, bacteria, and actinomycetes) were observed (Runion *et al.*, 1993).

Influences of atmospheric CO_2 on plants (carbon input and C:N ratio) and on soil microbes (composition and activity) will also impact carbon turnover and storage in soils. Lamborg *et al.* (1983) speculated that increased carbon input from increased biomass would lead to increased decomposition of organic matter and, thus, elevated atmospheric CO_2 would not result in accumulation of carbon 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 carbon. The debate remains unresolved, but studies are beginning to address this important issue. Mellilo (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 rates of decomposition and decreased soil fertility. Lekkerkerk *et al.* (1990) found the 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 nitrogen 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 carbon mineralization of 30% for CO_2-enriched material. An increase in carbon turnover was also observed in soils which had supported CO_2-enriched cotton plants for three seasons (Wood *et al.*, 1993) and could be related to increases in soil microfauna and saprophagous nematode populations (Runion *et al.*, 1993).

There is little doubt that increasing levels of atmospheric CO_2, along with other potential effects of global change, will impact soils and soil resources. This issue is beginning to receive serious attention (Arnold *et al.*, 1990; Bouwman, 1990; Buol *et al.*, 1990; Hatfield, 1990; Sombroek, 1990; Schlesinger, 1991) that must be continued.

FUTURE RESEARCH TARGETS

General research recommendations have been outlined by various authors (Strain & Cure, 1985; Mooney, 1991; Rogers & Dahlman, 1993). The research community has been repeatedly urged to explore root, rhizosphere, and soil phenomena. But what are the priority belowground targets? Since so little definitive work has been completed, unknowns cannot be delineated with certainty. As specific points from which to start, we propose the following *hypotheses* as objectives of future research.

Hypothesis 1. Exposure of plants to elevated atmospheric CO_2 will induce root proliferation and this in turn will accelerate bedrock weathering and consequently affect the rate of soil genesis.

Hypothesis 2. Plant (including root) growth stimulated by high CO_2 will lead to a slowing of soil erosion.

Hypothesis 3. Rhizosphere population composition and dynamics will be stimulated and altered under plants growing in high CO_2 atmospheres.

Hypothesis 4. The quality of plant tissue (roots, stems, leaves, and reproductive parts), especially in natural ecosystems, will be altered (e.g. C:N ratios) by extra CO_2 leading to changes in the rate of decomposition and an alteration in soil biological dynamics, especially carbon flux.

Hypothesis 5. Changes in root system architecture (i.e. root depth densities) of plants growing under enhanced CO_2 conditions will change the distribution of carbon in the soil profile.

Hypothesis 6. Atmospheric CO_2-induced differences in root tissue quality, rhizodeposition, and the rhizosphere will lead to either more or less susceptibility to root pathogens.

Hypothesis 7. Root growth patterns, if different at increased CO_2 concentrations, mean that water absorption from the soil profile will be different.

Hypothesis 8. Nutrient mining of the soil profile by root systems (of plants whose growth has been improved by CO_2 enrichment) will be affected.

Hypothesis 9. Root nutrient uptake kinetics (i.e. rate constants) will change under conditions of high CO_2 as a result of not only rhizographical alterations but also differences in root tissue characteristics.

Hypothesis 10. Shifts in litter quality and quantity, rhizodeposition, enhanced and altered microbial activity, and water/nutrient sorption patterns brought about by additional aerial CO_2 will lead to changes in soil physical properties such as structure, aggregation, and strength.

Hypothesis 11. If mineralization including N-fixation increases along with rising CO_2, many plant systems will respond with increased growth.

Hypothesis 12. Rhizodeposition will increase, and types and amounts of organic and inorganic chemicals released from roots of plants under high CO_2 conditions will change.

Hypothesis 13. Stimulation of very early seedling root growth by CO_2 enrichment will mean better establishment, and thus better survival, of crops.

Hypothesis 14. Root competition among species will be altered if CO_2 concentration increases.

Hypothesis 15. Enhanced rooting brought about by elevated CO_2 will lead to better plant growth under the impact of edaphic stress factors such as soil compaction.

These *hypotheses* represent major unknowns. We believe they should be tested.

CONCLUSION

Warnings of global change abound, and rightfully they should. Nevertheless, many agricultural researchers are optimistic, perhaps revealing their kinship with farmers. Certainly natural ecosystems and our soil, water, and air resources must be protected, but first mankind must be fed, fed from an agriculture which thrives or flounders upon environmentally derived inputs. Strategies designed to assure future world food security in a changing global environment must include a consideration of crop responses to elevated atmospheric CO_2. Regarding global change and the world food supply, Paul Erhlich put it this way, 'Enormous attention should be paid to agriculture, and it's just not happening' (Moffat, 1992). Certainly the resource base upon which all food production depends must be closely monitored within the framework of the greatest experiment in history. Our well-being and our economic welfare really depend upon both natural and agricultural plant systems, systems that are tuned to the influx of atmospheric CO_2 and changes in related factors.

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APPENDIX

Nomenclature of common and Latin names of plant species

Common name	Latin name
Alfalfa	*Medicago sativa*
Amaranthus	*Amaranthus* sp.
Aster	*Aster* sp.
Atlas cedar	*Cedrus atlantica*
Austrian pine	*Pinus nigra*
Broomsedge	*Andropogon virginicus*
Chrysanthemum	*Chrysanthemum morifolium*
Clover	*Trifolium* sp.
Corn	*Zea mays*
Cotton	*Gossypium hirsutum*
Curly dock	*Rumex crispus*
French bean	*Phaseolus vulgaris*
Loblolly pine	*Pinus taeda*
Maize	*Zea mays*
Okra	*Hibiscus esculentus*
Orchard grass	*Dactylis glomerata*
Pea	*Pisum sativum*
Peperomia	*Peperomia* sp.
Perennial rye grass	*Lolium perenne*
Pineapple	*Ananas comosus*
Potato	*Solanum tuberosum*
Radish	*Raphanus sativus*
Raspberry	*Rubus idaeus*
Rice	*Oryza sativa*
Shortleaf pine	*Pinus echinata*
Sorghum	*Sorghum vulgare*
Soybean	*Glycine max*
Sudan grass	*Sorghum sudanense*
Sugar beet	*Beta vulgaris*
Sugarcane	*Saccharum officinarum*
Sweet potato	*Ipomoea batatas*
Sweetgum	*Liquidambar styraciflua*
Tomato	*Lycopersicon esculentum*
Virginia pine	*Pinus virginiana*
Wheat	*Triticum aestivum*
White clover	*Trifolium repens*
White oak	*Quercus alba*
Winter wheat	*Triticum aestivum*
Yellow poplar	*Liriodendron tulipifera*