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REVIEW

Plant responses to high CO_2 concentration in the atmosphere

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Abstract

The impact of continuous rise in ambient CO_2 concentration (AC) in the atmosphere on different facets of growth of crop plants is assessed. The effects of CO_2 enrichment (EC) on plant growth, C_3 and C_4 photosynthesis, source-sink ratio, partitioning and translocation of metabolites, photosynthetic enzymes, respiratory rate, leaf area index, stomatal conductance (g_s), transpiration rate, biomass production and water use efficiency are reviewed. The CO_2 fertilization effects are studied in both short-term (open top chambers) and long-term experiments. Long-term experiments suggest that ribulose-1,5-bisphosphate carboxylase is inactivated at high CO_2 concentrations. Also g_s is lowered. One of the conspicuous effects of EC is the closure of stomata in C_3 plants. Photosystem (PS) 2 electron transport is more affected than PS1. Starch is the immediate product accumulated in the leaf of C_3 plants. The "CO_2 fertilization effect" does not confer any great advantage even in C_3 plants.

Additional key words: biomass; growth; leaf area index; photosystems; ribulose-1,5-bisphosphate carboxylase; sink-source ratio; stomatal resistance; transpiration; water use efficiency.

Introduction

As global population increases and industrialization expands, CO_2 and toxic air pollutants are expected to be injected into the atmosphere at increasing rates (Allen 1990). Atmospheric carbon dioxide concentration has increased from about 280 to 350 cm^3 m^{-3}(air) from *ca.* 1750 to the present day. It is currently increasing at the rate of 1.2-1.4 cm^3 m^{-3} $year^{-1}$ and is expected to continue to do so into the next century (Allen 1989, Lashof and Tirpak 1989). Most of the recent rise is attributable to burning of fossil fuels (Rotty and Masters 1985). Some scenarios predict that atmospheric CO_2 could double within 100 years (Allen 1990). The CO_2

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concentration before 1800 was around 265-280 μmol mol^{-1} based on ice core and tree ring data (Stuiver *et al.* 1984, Raynaud and Barnola 1985, Oeschger and Stauffer 1986). Box models of oceans suggest that 60-70 % of the CO_2 released remains in the atmosphere with the remainder incorporated in the oceans (Baes and Mulholland 1985). General circulation models have predicted average global surface air warming of 1.5 to 5.2 °C, if the AC doubles (Carbon Dioxide Assessment Committee 1983, Mitchell 1989, Allen 1990). In this review article, the effects of EC in the atmosphere on different facets of plant physiology are presented.

Growth and biomass

Mbikayi *et al.* (1983) reported that the growth and development of cowpeas showed positive responses to EC. Plant height increased rapidly with EC. The production of leaves was greater in EC than in plants grown at 354 $cm^3(CO_2)$ m^{-3}. Bhattacharya *et al.* (1985a,b) also reported a significant increase in plant height, leaf numbers and leaf expansion in sweet potatoes and cowpeas grown at EC under controlled environment. Plant height in soybean either was unaffected by EC or showed only small increases (Rogers *et al.* 1980, 1983a,b). Studies conducted with white pine (Funsch *et al.* 1970) and crab apple seedlings (Krizek *et al.* 1970, 1971) showed that EC resulted in increase in height and the production of lateral branches.

Fresh and dry masses of whole cowpea plants also increased at EC, as compared to plants grown at AC in the open top chamber. The increase in biomass production as a result of EC is reported (Krizek 1984, Strain and Cure 1986) but the relative increase of dry mass varies with plant species (Strain and Cure 1985, Reining 1995). Mbikayi *et al.* (1983) reported that increased production of biomass at EC was associated with increased net assimilation rate (NAR) and relative growth rate (RGR).

Acock and Allen (1985) observed increasing above-ground biomass (18 %) and decreasing evapotranspiration with increasing carbon dioxide. Cure (1985) showed that in rice, maize, and soybean, NAR and biomass accumulation responded about 40 % more to a doubling of CO_2 concentration when grown under day/night temperatures of 28/23 °C than under 23/20 °C. Idso *et al.* (1987a) reported that the biomass:growth ratio for a 300 μmol mol^{-1} increase in CO_2 increased somewhat linearly with increasing temperature (0.087 per °C) over a range of 19 to 34 °C for several plants. Close association of dry matter accumulation with leaf area was observed by Poskuta and Nelson (1986) at high CO_2 concentration (Nijs *et al.* 1989b). In wheat, Kendall *et al.* (1985) found little or no enhancement of dry matter gain for several cultivars grown at 1200 $cm^3(CO_2)$ m^3, which indicated that photosynthesis was not inhibited (Du Cloux *et al.* 1989).

Nijs *et al.* (1989a) reported that at EC allocation towards the root system became greater in the course of canopy development of *Lolium perenne*, while stimulation of shoot dry-matter accumulation was inversely affected. Over an entire growing season the root/shoot production ratio was 22 % higher under EC than at AC (Nijs *et al.* 1989a). Several studies showed that the extra C in plant leaves induced by EC

resulted in an increase in leaf size, number of branches (or tillers) and number of nodes along the branches which support leaves, and hence greater leaf area (Rogers *et al.* 1984a, Bhattacharya *et al.* 1985a,b, Allen *et al.* 1988, Allen 1990). Leaves also respond to EC by an increase in specific leaf mass (SLM, dry mass per unit leaf area). The increase in SLM is related to the stored starch in leaves (Thomas and Harvey 1983, Huber *et al.* 1984a, Bhattacharya *et al.* 1985a, Allen *et al.* 1988, Allen 1990).

The CO_2 enrichment of rice increases dry mass (Imai and Murata 1979a), plant height (Imai and Murata 1979b), tillering (Imai and Murata 1976) and yield (Cock and Yoshida 1973, Yoshida 1973). The increased tillering was due to producing tillers at lower nodes, where the AC plants failed to produce a tiller (Imai and Murata 1976). The increased yield was due to an increase in panicles per unit land area, which resulted in an increase in grains. Yoshida (1976) concluded that the optimum CO_2 concentration for growth and yield in rice was between 1500 and 2000 μmol mol^{-1}. Cock and Yoshida (1973) reported that the pre-anthesis treatment increased grain number per unit land area and grain mass, whereas the post-anthesis treatment increased percentage of filled-grains and grain mass with unaffected grain number per unit land area. *Sorghum*, a C_4 plant, showed no height or leaf number response to EC but showed consistent leaf, stem, root and grain dry mass increases across 485, 660 and 795 μmol(CO_2) mol^{-1} as compared with a 330 μmol mol^{-1} control (Chaudhuri *et al.* 1986). Young trees and tree crops generally show positive growth responses to EC (Tolley and Strain 1984, Luxmore *et al.* 1986, Norby *et al.* 1986, Downton *et al.* 1987, Koch *et al.* 1987, Brakke 1989). Although C_4 plants in general are not expected to respond to EC as much as C_3 plants (Pearcy and Björkman 1983), several experiments show positive responses of C_4 grasses to EC (Riechers and Strain 1988, Allen 1990).

At warm season, C_4 grasses have the highest shoot dry mass under EC. The shoot:root ratio does not change (Mo *et al.* 1992). Cold-adapted plants show little response to EC, and only some species show a decline in biomass accumulation. The number of leaves, total length of stem, total leaf area, overall growth rate, total leaf, stem and root dry masses responded positively to EC (700 μmol mol^{-1}), but the leaf size and biomass allocation did not change with EC (Radoglou and Jarvis 1990, Baxter *et al.* 1994a,b). There was a significant decrease in shoot relative to root growth at EC (680 μmol mol^{-1}) in *Festula vivipara* the leaves of which also markedly discoloured and more rapidly senescenced (Baxter *et al.* 1994a,b).

Root growth is enhanced following increased cell expansion in EC in *Sanguisorba minor, Lotus corniculatus, Anthyllis vulneraria* and *Plantago media* (Ferris and Taylor 1994). The elongation rate of individual root axes was not affected but there was significant increase in the number of actively growing roots, 65 % more at 800 than at 330 $cm^3(CO_2)$ m^{-3}. CO_2 enrichment also increases root biomass (Baker *et al.* 1990). The EC increased root dry mass, particularly of droughted crops indicating that high CO_2 can compensate for decreased root growth under drought. However, the root dry matter of sweet potato increased more with EC in well watered than droughted plants (Bhattacharya *et al.* 1990, Lawlor and Mitchell 1991). Under high

water supply and high nitrogen nutrition EC did not affect the root/shoot ratio (Peñuelas *et al.* 1995b).

The CO_2-induced increases in leaf area are largely due to more extensive branching in dicotyledonous plants (Rogers *et al.* 1984a) and tillering in grasses (Sionit *et al.* 1981), although there is also an increase in expansion rates and a small increase in maximum leaf size (Cure *et al.* 1989, Lawlor and Mitchell 1991). There is little evidence from field studies on the extent to which increases in leaf area could be obtained due to EC as seen in soybean (Rogers *et al.* 1983a). The SLM increased in response to EC in soybean (Rogers *et al.* 1983a, Lieth *et al.* 1986, Leadley and Reynolds 1988) and sweet potato (Biswas and Hileman 1985) but not in maize (Rogers *et al.* 1983a). The increase in SLM is presumably due mostly to the increase in starch content (Huber *et al.* 1984b) as discussed but the leaves of soybean plants grown at EC are also thicker due to an increase in the number of palisade cells, an effect which does not occur in maize (Thomas and Harvey 1983, Lawlor and Mitchell 1991).

The number of nodules increased significantly in cowpea plants grown at 655 $cm^3(CO_2)$ m^{-3}. The size of the nodules was also greater at EC than AC suggesting a positive correlation between CO_2 and the availability of nitrogen through symbiotic fixation. Rogers *et al.* (1983b) and Finn and Brun (1982) reported an increase in the total nodule mass per plant in soybeans; increased nodule activity at EC might have resulted in a general increase in growth of the plants (Mbikayi *et al.* 1983).

Stomata

Mbikayi *et al.* (1983) reported that stomatal density was greater on the abaxial than adaxial surface of the leaves of cowpea plants. The number of stomata increased at EC as compared to AC-grown plants in open top chambers. The increased number of stomata could be associated with the production of smaller leaves at EC during middle of the growth period. In *Phaseolus vulgaris*, both the leaf area and total number of stomata per leaf were significantly greater at EC than AC (O'Leary and Knecht 1981). Moss *et al.* (1961) also reported that stomatal aperture was reduced in maize exposed to 535 and 575 $\mu mol(CO_2)$ mol^{-1} compared to 260 and 310 $\mu mol(CO_2)$ mol^{-1} (Allen 1989). Nevertheless, stomata acclimate to long-term exposure to EC (Chen *et al.* 1995). The leaves in 660 $cm^3(CO_2)$ m^{-3} in air developed a greater area and specific mass and contained more stomata, epidermal cells and chlorophyll per unit leaf area. Leaves developed in AC demonstrated a significant regrowth with increased cell and stomatal number when exposed to EC (Gaudillère and Mousseau 1989).

Decreased g_s with increasing CO_2 has been documented for maize, soybean and sweet gum (Mbikayi *et al.* 1983, Rogers *et al.* 1983a). Moreover, decreased g_s in EC-grown plants has been associated with an increase in water use efficiency (WUE) (Rogers *et al.* 1983b). In many cases high CO_2 concentration decreases transpiration rate (E) through an increase in stomatal resistance (Goudriaan and Van Laar 1978, Farquhar and Sharkey 1982, Rogers *et al.* 1983b). Reports of CO_2 stomatal responses

range from complete insensitivity to CO_2 concentration between 0-2000 cm^3 m^{-3} in cotton (Bierhuizen and Slatyer 1964) and Scotch pine (Ng 1978) to a ten-fold decrease in g_s in response to an increase in CO_2 from 300 to 500 cm^3 m^{-3} in apple leaves (Warrit *et al.* 1980). The negative effects of EC are more intense under high water availability (Peñuelas *et al.* 1995a).

The g_s decreases with increasing CO_2 concentration in most of the studies of over 50 species although in a few cases no response or very large response has been reported (Morison 1985, 1987, Allen 1990, Liang *et al.* 1995). Stomatal density may decrease with increasing CO_2 concentration in some species (Woodward and Bazzaz 1988), but other reports indicate no significant change (Körner 1988) or increases of stomatal density with EC (O'Leary and Knecht 1981, Thomas and Harvey 1983). Gaastra (1959) and Pallas (1985) showed that leaf E of several species decreased as CO_2 concentration increased. Furthermore, Gaastra (1959) showed that leaf temperature increased as E was decreased by EC. Allen *et al.* (1985) pointed out that leaf and canopy temperature should rise as CO_2-induced stomatal closure expresses itself under EC (Allen 1990).

Stomatal behaviour is the major barrier for both CO_2 and water vapour transport as well as an important determinant of leaf WUE. The WUE is defined herein as the ratio of net photosynthetic CO_2 exchange rate (P_N) to E (Nijs *et al.* 1989a,c, Allen 1990). Plant canopy WUE may either be reduced by EC (Rogers *et al.* 1984a,b,c, Jones *et al.* 1985c,d, King and Greer 1986) or be essentially unaffected by CO_2 (Kimball *et al.* 1983, 1984, Jones *et al.* 1985b,d, Allen 1990). Leaf area per plant or leaf area index (LAI) was greater with increasing CO_2 (Allen 1990). Although WUE is approximately doubled by a doubling of CO_2, most of the increase in C_3 plants comes from an increase in P_N with only a small contribution from reduction in E (Acock and Allen 1985, Allen *et al.* 1985, Jones *et al.* 1985b,d, Valle *et al.* 1985a,b). High CO_2 concentration alleviates water stress effects in several plant species, *e.g.*, in sweetgum (Tolley and Strain 1984), soybean (Rogers *et al.* 1984c), and wheat (Gifford 1979, Sionit *et al.* 1980). Nijs *et al.* (1988) conclude that long-term EC treatment favours the survival of *L. perenne* and *Trifolium repens* when exposed to severe rapidly developing drought stress (Allen 1990). The mean increase in dry matter production of 33 % for a doubling of AC (Kimball and Idso 1983) across a wide range of C_3 crops, and the 34 % decrease in water loss results in much greater WUE. In field studies this has been substantiated in several species including soybean in which WUE increased 2- to 4-fold when grown in 800 compared to 300 $cm^3(CO_2)$ m^{-3} (Jones *et al.* 1985b, Allen 1990).

P_N

Several reviews and assessments of the response of plants to rising concentration of atmospheric CO_2 have been published (Pearman 1980, Kimball 1983, Lemon 1983, Strain and Cure 1985, Enoch and Kimball 1986, Allen 1989, 1990, Kimball *et al.* 1989). In C_3 plants growing under adequate irradiance, photosynthesis requires 800-1000 $cm^3(CO_2)$ m^{-3} for saturation. However, photosynthesis of C_4 plants under

adequate irradiance is almost saturated at current AC (Lawlor and Mitchell 1991). Therefore, EC increases P_N and dry matter production of C_3 plants substantially, with little or no effect on C_4 plants. Reviews by Kimball (1983) and Cure and Acock (1986) of experiments done under a wide range of conditions show that doubling AC from *ca.* 330 to 650 $cm^3(CO_2)$ m^{-3} increases the productivity of a large number of C_3 crop plants on an average by 33 %. Given the increasing ACs over the last *ca.* 250 years, an increase in the productivity of vegetation, either natural or agricultural, would be expected. Quantitative assessment of such effects is difficult because of the variation in weather and other environmental factors (*e.g.*, nutrition - Lawlor and Mitchell 1991). Given the average response of crops to EC determined in short-term experiments, the increase in AC from 280 to 350 cm^3 m^{-3} would be expected to increase the dry matter production of crops by only some 8-10 %. This would be difficult to determine against the variation caused by other factors. Therefore, we must rely for assessement of the effects of global increase in CO_2 on experiments on plants exposed to local EC concentrations (Lawlor and Mitchell 1991).

In *Eucalyptus microtheca* and *E. polyanthemus*, dark respiration rate (R_D) dropped by approximately 50 % for a doubling of the AC, while P_N rose by a factor of two (Idso and Kimball 1993). The EC plants had higher concentrations of starch in their leaves and roots than the AC plants. The g_s was lower in the EC plants (Tuba *et al.* 1994). The higher WUE in the EC wheat plants was the result of a larger decrease in E in the EC plants than in the AC plants (Tuba *et al.* 1994). Despite these physiological and biochemical considerations, the P_N are not always greater in CO_2 rich environments. Often plants growing under such conditions initially show increased P_N but over time this rate falls and approaches that of plants growing under today's CO_2 concentration (Marek *et al.* 1995). The reasons for this decline are unclear but several mechanisms have been proposed (Bazzaz and Fajer 1992).

The biochemical pathway of photosynthetic carbon metabolism influences the responses of plants to CO_2 (Tolbert and Zelitch 1983, Allen 1989). C_4 plants have a more efficient photosynthetic apparatus than the C_3 plants at the present atmospheric concentrations of CO_2 (350 μmol mol^{-1}) and do not increase P_N as much as C_3 plants in response to EC (Allen 1989). In general, C_3 plants show increased P_N at the leaf level and whole canopy level when grown at EC (Jones *et al.* 1985a, Valle *et al.* 1985b) but sometimes reduced P_N values have been reported when plants or canopies are exposed to EC for prolonged intervals (Oechel and Strain 1985, Peet *et al.* 1986, Tissue and Oechel 1987). The probable cause of reductions in P_N after prolonged exposure to EC is an excess of photoassimilate production in leaves with respect to photoassimilate utilization by the plant or crop system (Allen 1989). The process of P_N reduction under high CO_2 (and other conditions where source exceeds sink) is sometimes referred to as end-product feedback inhibition of photosynthesis. Some progress has been made in identifying potential enzymatic regulation of photosynthetic feedback inhibition but this could become an important area of future research (Allen 1989).

In some cases, growth of plants at EC has resulted in reduction of photosynthetic capacity and ribulose-1,5-bisphosphate carboxylase (RuBPC) activity (Baker *et al.* 1988) but in another case photosynthetic capacity was increased (Campbell *et al.*

1988). Increases in leaf thickness and number of cells per unit leaf area (Vu *et al.* 1989) may contribute to greater photosynthetic capacity (Allen 1989).

Moss *et al.* (1961) exposed field-grown maize plants to four concentrations of CO_2 across a wide range of solar irradiance. They showed a slightly more than 10 % increase in P_N for a doubling of AC. Rogers *et al.* (1983a) reported that sweet corn leaf P_N decreased about 4 % with a doubling of concentration from 330 to 660 μmol mol^{-1}. Allen (1990) pointed out that at AC the photosynthetic rates of C_4 plants tend to increase with temperature to a greater extent than those of C_3 plants. High concentrations of CO_2 can give C_3 plants a P_N *vs.* temperature response that is similar to that in C_4 plants. The P_N of sugarcane leaves and plant canopies should increase with air temperature at least upto a critical point. The P_N and biomass production of C_4 plants under doubled CO_2 may also be increased by about 10 % (Allen 1989).

Increasing the AC above 600 cm^3 m^{-3} triggers different reactions in the plant (Nijs *et al.* 1989b): thus stomatal closure may reduce P_N but a larger gradient between chloroplast and AC will counter this effect. The R_D exerts an impact on the P_N-yield relationship: *e.g.*, the *L. perenne* cultivars with a low leaf R_D have higher dry matter yields than cultivars with high R_D (Wilson 1982, Nijs *et al.* 1989a,b,c).

Table 1. Stimulation of net photosynthetic rate (P_N) in mature leaves at growth CO_2 concentration in plants which have acclimatized to enhanced (70-100 Pa) CO_2. The results are in per cent of the rate found for plants growing in air (33-35 Pa CO_2). From Stitt (1991).

Species	P_N	References
Soybean	200	Clough *et al.* (1981)
	161	Havelka *et al.* (1984a)
	295	Campbell *et al.* (1988)
	153	Cure *et al.* (1989)
Potato	202	Sage *et al.* (1989)
Cotton (high N)	150	Wong (1979)
Vine	135	Kriedemann *et al.* (1976)
Chenopodium album	111	Sage *et al.* (1989)
Bean	102	Caemmerer and Farquhar (1984)
	104	Sage *et al.* (1989)
Tomato	120	Ho (1977)
	102	Yelle *et al.* (1989a)
	103	Besford *et al.* (1990)
Cucumber	105	Peet *et al.* (1986)
Water hyacinth	99	Spencer and Bowes (1986)
Tobacco	78	Raper and Peedin (1978)
Brassica oleracea	77	Sage *et al.* (1989)
Cotton (low N)	78	Wong (1979)
Soybean (sinks removed)	100	Clough *et al.* (1981)

The leaf P_N increases when C_3 crop plants are exposed to long-term EC (Allen 1990). Table 1 summarizes the P_N values at growth CO_2 concentration for a selection of species after several weeks growth in AC or EC (70-100 Pa) (Stitt 1991). A small

but significant increase was still found in potato, soybean and cotton. These results raise the following questions: (*1*) What is responsible for the long term suppression of photosynthesis in enhanced photosynthesis? (*2*) Why is the response so variable?

A linear response of soybean leaves to EC was reported when plants were grown at CO_2 concentrations from 340 to 910 μmol mol^{-1} (Rogers *et al.* 1983a). Valle *et al.* (1985 a,b) confirmed this type of response for soybean leaflets grown at and exposed to two levels of CO_2, 330 and 660 μmol mol^{-1}. Wheat plants enriched to 1390 μmol mol^{-1} had 50 % higher P_N of the flag leaf than wheat grown at 332 μmol(CO_2) mol^{-1} (Havelka *et al.* 1984a). Although these wheat plants did not respond to EC as well as soybean, they still showed positive responses to EC. However, other crop plant photosynthetic responses decrease following an initial stimulation by EC (Kramer 1981, Wulff and Strain 1982). Monoecious cucumbers (*Cucumis sativus* L.) exposed to continuous EC showed reductions in P_N and no increase in yields (Peet *et al.* 1986). This type of acclimation is common in many ecosystem species where the initial stimulation of P_N by EC decreases to the point where leaf or canopy P_N becomes similar to that at AC (Oechel and Strain 1985, Tissue and Oechel 1987, Allen 1990). A reason for lack of response to EC is end-product feedback inhibition of P_N due to imbalances of 'sink' for photoassimilate relative to source of photoassimilate. This feedback inhibition is usually manifest by the accumulation of starch in the chloroplasts of leaves (Madsen 1968a,b, Hofstra and Hesketh 1975, Nafziger and Koller 1976, Mauney *et al.* 1979, Clough *et al.* 1981). End-product feedback inhibition has been variously attributed to disruption of the grana of chloroplasts by starch grains (Cave *et al.* 1981), inhibition of RuBPC activity by phosphorylated sugars *via* competition with RuBP for binding sites (Bowes and Ogren 1972), some mechanism for inhibition of sucrose phosphate synthetase (SPS), which would result in photosynthetic starch formation at the expense of photosynthetic sucrose formation (Huber 1983), or some mechanism mediating the availability of phosphate at the chloroplast membrane (Hesketh *et al.* 1983, Allen 1990). Experiments with soybean indicate that the sink for photoassimilates (vegetative or reproductive growth) should always be large enough for EC to maintain higher leaf P_N (Jones *et al.* 1984, 1985a,b,c,d, Acock *et al.* 1985). Field experiments with cotton showed consistent large photosynthetic (Radin *et al.* 1987) and yield responses to CO_2 (Kimball *et al.* 1984, 1986, Kimball 1986). Rice canopy P_N and yield responses to CO_2 increased to a concentration of 500 μmol mol^{-1} but tended to level off at higher concentrations (Baker *et al.* 1988). RuBPCO content and activity also tended to decrease with EC (Baker *et al.* 1988). Although P_N per unit leaf area of maize (C_4 plant) does not increase with EC (Rogers *et al.* 1983a), yields of these plants slightly increase (Rogers *et al.* 1983a, Surano and Shinn 1984, King and Greer 1986, Allen 1990). These increases may be related to better water relations due to a partial stomatal closure. Cotton leaves showed a linear relation of P_N with intercellular CO_2 concentration across a wide range of CO_2 treatments throughout most of the growing season. The leaf-area-basis and canopy-area-basis P_N values show very large ranges of response depending upon species, growth conditions, length of exposure and nutrient levels (De Lucia *et al.* 1985). Cure (1985) summarized the effect of doubling AC on P_N of nine crops (wheat, barley, rice,

maize, sorghum, soybean, alfalfa, cotton, potato, and sweet potato) by comparing the per cent increase at 680 μmol mol^{-1}.

A simple biochemically based model of photosynthesis was coupled to a model of g_s to calculate the response of P_N to EC (Kirschbaum 1994). Photosynthesis was much more responsive to CO_2 at high than low temperatures. As P_N was far from being saturated at the current AC, considerable further gains in P_N were predicted through continuing increase in CO_2 concentration. The strong interaction with temperature also leads to photosynthesis in different global regions experiencing very different sensitivities to increasing CO_2 concentrations. A continuous increase in CO_2 concentration may lead to enhanced primary productivity (Kirschbaum 1994). The basis of this response lies in the sensitivity of the photosynthesis of C_3 plants to CO_2 concentration. The P_N is significantly more sensitive to CO_2 at higher temperatures than at lower temperatures. Consequently, growth responses to EC would also be expected to be much more pronounced at higher than at lower temperatures (Rawson 1992). Enhanced productivity due to EC would lead to additional carbon sequestration and offset losses of carbon due to increasing temperature (Kirschbaum 1994).

The interaction between CO_2 and temperature also has to be taken into account in the interpretation of experimental results. The responses to EC were small in experiments with tundra vegetation (Billings *et al.* 1984, Tissue and Oechel 1987) but large and persistent in the much warmer vegetation of a salt marsh in Maryland, U.S.A. (Curtis *et al.* 1989, Drake 1992). Differences in nutrient availability may account for most of the differences in response but different inherent CO_2 sensitivities at different temperatures would have further compounded the different responses to CO_2 enrichment (Kirschbaum 1994). Growth is essentially determined by the rate of diffusion of CO_2 into the leaf, which, in turn, is limited by the availability of water for diffusion out of the leaf. At a particular location where C_3 and C_4 plants co-exist, they must compete for other limiting resources, such as water, nutrients or access to radiant energy. Increasing CO_2 concentration confers a selective advantage on the C_3 plants and puts them into an increasingly favourable competitive position. Increased carbon gain by C_3 plants would allow them to either increase root growth and complete more successfully with their C_4 neighbours for nutrients, or increase foliage production to compete more successfully for available radiation (Kirschbaum 1994). The continuously improving photosynthetic performance of C_3 plants should put great competitive pressure on neighbouring C_4 plants, especially in warmer regions where the improvements in the performance of C_3 plants should be most marked (Kirschbaum 1994).

When air-grown cells of *Chlorococcum littorale* were enriched with CO_2, growth was enhanced after a lag period of one to two days at 20 % CO_2, and of 3 to 6 d at 40 % CO_2 (Pesheva *et al.* 1994). Changes in P_N, measured as oxygen evolution and CO_2 fixation, were similar to those observed for growth. During the initial inhibition of photosynthesis in 40 % CO_2, the activity of PS2 was suppressed. In contrast, the PS1 activity was greatly enhanced. Air-grown cells of *C. littorale* possessed comparatively high carbonic anhydrase (CA) activity which was localized inside the cells and on the cell surface. Under EC, extracellular CA activity was greatly

suppressed and intracellular activity almost completely abolished. The PEPC activity was higher in EC-grown cells than in AC cells. The above results indicated that the lag phase induced by 40 % CO_2 was due to suppression of PS2 activity.

Adaptation of microalgae to low CO_2 concentrations (air, 0.04 % CO_2) has been intensively studied. Growth under low CO_2 concentrations is associated with increased affinity for external inorganic carbon which is caused by high CA activity for concentrating inorganic carbon inside the algal cells. These two factors enhance the supply of CO_2 to RuBPCO and thus increase the carboxylation reaction, while reducing the oxygenase activity. *C. littorale* is a new unicellular marine green alga, which can grow rapidly under CO_2 concentrations as high as 60 %. This species enables to study the influence of very high CO_2 concentrations on algal photosynthesis. When cells grown in air containing 0.04 % CO_2 (low CO_2-cells) are transferred to high CO_2, the cells start to grow again after a lag period the length of which is dependent on the new CO_2 concentration. To understand the direct short term effect of EC on P_N in C_3 plants, it must be understood to what extent the EC will stimulate or relieve demand on partial processes like carboxylation, light harvesting and electron transport, the Calvin cycle, and end-product synthesis, and the extent to which these various processes actually control P_N (Stitt 1991). The control is more effected by RuBPCO (which responds sensitively to CO_2) than by other components, and therefore, photosynthesis is stimulated by 25-75 % when the CO_2 concentration is doubled from 35 to 70 Pa (Stitt 1991).

Most plants undergo a gradual inhibition of photosynthesis during acclimation to EC. This is related to an inadequate demand for saccharides in the remainder of the plant. Differences in the long-term response to CO_2 may be explained by differences in the source-sink status of plants, depending upon the species, the developmental stage, and the developmental conditions (Stitt 1991). Accumulating saccharides could lead to a direct inhibition of photosynthesis, involving mechanical damage by large starch grains or P_i-limitation due to inhibition of sucrose synthesis. P_i is important in the short-term regulation of C partitioning to sucrose and starch, but its contribution to the 'sink' regulation has not yet been conclusively demonstrated. Indirect or 'adaptive' regulation of photosynthesis is probably more important, involving decreases in the amounts of key photosynthetic enzymes, including RuBPCO. This decreases P_N, and potentially would allow resources (*e.g.*, amino acids) to be remobilized from the leaves and reinvested in sink growth to readjust the source-sink balance. Changes of RuBPCO and possibly of other proteins are also involved during acclimation to high CO_2 (Stitt 1991). The EC stimulates the carboxylation reaction catalysed by RuBPCO. Potentially, this allows higher P_N, and will provide more saccharides for plant growth. However, the rest of the plant may, for various reasons, be unable to utilize or store these additional saccharides. In this case, long-term and indirect effects may appear, in which feedback regulation leads to an inhibition of photosynthesis (Stitt 1991). Therefore, the planning and interpretation of experiments on EC must clearly distinguish between the short- and long-term effects of CO_2. The EC frequently leads to a larger stimulation of photosynthates in young seedlings of soybean, cotton, sunflower, and tomato than in older plants (Ho 1977, Mauney *et al.* 1978, Ackerson *et al.* 1984, Radin *et al.* 1987, Stitt 1991).

In the short-term, the response depends on what controls the current rate of photosynthesis. Considerable advances have been made in understanding the short-term regulation of photosynthesis, and in identifying and quantifying factors which control the P_N. In the long-term, the ability of the leaf to maintain high P_N will depend upon the sink-source status of the whole plant and how this is regulated. This will vary considerably depending upon the species, its habitus and physiology, and the environmental conditions (Stitt 1991). Therefore, physiological and biochemical mechanisms that regulate sink-source interactions will be an important target for research in the future. Such studies will provide insights into the long-term response of plants to EC (Stitt 1991).

Assimilate partitioning

No clear trend is evident from the controlled environment studies on the effect of EC on the distribution of dry matter between organs, with the exception of tubers, which become a bigger proportion of plant dry mass at high CO_2 (Lawlor and Mitchell 1991). No significant effect of EC is seen on the harvest index and root:shoot ratios reviewed by Cure and Acock (1986).

Root:shoot ratios tend to increase for CO_2-enriched herbaceous plants and decrease for CO_2-enriched trees. Root:shoot ratios for cereals tend to remain constant (Farrar and Williams 1991). Cereals often do not show long-term changes in the partitioning of assimilates between root and shoot in response to EC, but increases in root:shoot ratio have been observed for *Agrostis capillaris* and *Hordeum vulgare*. Similar increases in the long-term partitioning of assimilates to the roots due to EC have been reported for a wide range of herbaceous species, *e.g.*, *Abutilon theophrasti, Brassica pekinesis, Carex bigelowii, Glycine max, Ledum palustre* and *Lycopersicon esculentum* (Farrar and Williams 1991).

For tree saplings provided with sufficient nutrients, there is a decrease or no change in root:shoot ratio at higher CO_2 concentrations (Eamus and Jarvis 1989). Growth in limiting nutrients may promote an increase in partitioning to the root (Norby *et al.* 1987) and hence assimilate partitioning under high CO_2 may depend upon nutrient status (Lawlor and Mitchell 1991). *Eriophorum vaginatum* has a decreased root:shoot ratio with increasing CO_2 in the absence of any change in RGR (Tissue and Oechel 1987, Lawlor and Mitchell 1991).

In field studies, the increase in the proportion of total dry mass in tubers at EC was confirmed for sweet potato (Biswas and Hileman 1985, Bhattacharya *et al.* 1990) and for carrot and radish (Idso *et al.* 1988). No significant effect of EC on root:shoot ratio in cotton and soybean was found (Idso *et al.* 1988), while Chaudhuri *et al.* (1990) found a variable response of the root:shoot ratio in winter wheat to CO_2 although it generally declined with EC in water-stressed plants. The root:shoot ratio in rice generally increases with CO_2 concentration (Baker *et al.* 1990). An increase in harvest index due to EC was observed in cowpea (Biswas and Hileman 1985), but there was no effect on that in winter wheat (Havelka *et al.* 1984b). There were no significant changes in partitioning of dry matter among the leaves, stems or pods due

to CO_2 enrichment in soybean (Ackerson *et al.* 1984), although there was a slight decline in harvest index with EC (Rogers *et al.* 1986). Therefore, the extra growth induced by EC is generally distributed evenly between organs, implying that the mechanisms are not differentially affected by additional assimilates (Lawlor and Mitchell 1991).

Farrar and Williams (1991) report that in plants grown under AC the processes of sucrose transport to the phloem, loading into and unloading from the sieve tubes are not fully understood. No studies have as yet investigated these phenomena with respect to EC. Although there is consistent agreement in the literature that the EC promotes both the CO_2 fixation and the leaf starch accumulation, few studies have attempted to measure assimilate export from a CO_2 enriched leaf. According to Finn and Brun (1982) the majority of additional saccharides provided by short term (36 h) CO_2 treatment of 4-week-old soybean plants was retained in the leaf as starch and not exported to the roots and nodules. Similarly, although Ho (1977) reported a 78 % increase in the rate of assimilate export from the leaves of tomato plants grown for 4 weeks in 1000 $cm^3(CO_2)$ m^{-3}, such long-term CO_2-enrichment of both soybean and *Phaseolus* plants resulted in either little change or in a decrease in the rate of assimilate export (Huber *et al.* 1984a, Hoddinott and Jolliffe 1988, Farrar and Williams 1991). Long-term CO_2-enrichment of a mature alfalfa crop had little effect on P_N or dry mass accumulation, whilst alfalfa seedlings treated similarly increased their P_N and growth rate (Baysdorfer and Bassham 1985). Plant nutrient status is an important determinant of both the long-term and short-term responses to EC (Finn and Brun 1982, Eamus and Jarvis 1989, Marks and Clay 1990, Sage *et al.* 1990). Single leaf experiments overlook the possibility that the growth rate of the canopy may be greater for the EC plants. Therefore, the effect of assimilate export from a leaf on sink development may be amplified. However, two considerations borne out from this will have a major influence on partitioning within an EC plant (Farrar and Williams 1991): (*1*) The increase in leaf export rate should coincide with an increase in canopy development. (*2*) The source:sink ratio should be altered in the EC plants.

Farrar and Williams (1991) report that EC may decrease pools of glycine and serine and reduce the partitioning of recently fixed carbon into amino acids (Madore and Grodzinski 1984, 1985).

Total uptake of nutrients was, in general, greater in plants of *A. capillaris* and *Poa alpina* when grown at 680 $\mu mol(CO_2)$ mol^{-1}. In *Festuca vivipara*, however, the uptake was considerably reduced in plants grown at EC. Overall, a doubling of AC had little effect on the nutrient use efficiency or productivity of *A. capillaris*. In *P. alpina*, potasium, magnesium and calcium productivities (total plant dry mass gain per unit of nutrient) were significantly reduced and photosynthetic nitrogen and phosphorus use efficiencies were doubled at EC with respect to AC. *F. vivipara* grown at EC, however, showed large increases in the ratio of nonstructural saccharides to nitrogen content of leaves and reproductive tissues, indicating a substantial imbalance between the production and utilization of assimilates (Baxter *et al.* 1994a,b).

Plant composition

Several field studies have addressed the question of whether EC affects the composition of plants (Lawlor and Mitchell 1991). Nor was any enrichment effect observed on the moisture, fibre, oil, protein or fatty acid composition of maize and soybean seeds (Rogers *et al.* 1983a,b, 1986). Havelka *et al.* (1984b) found no change in the N content per unit dry matter in leaves, stems or grain due to EC in winter wheat. The EC increased the saccharide status (starch, sucrose and glucose) of soybean under field conditions (Ackerson *et al.* 1984, Havelka *et al.* 1984a). Wheat accumulated double amounts of sucrose and starch in 1200 $cm^3(CO_2)$ m^{-3} compared with 340 $cm^3(CO_2)$ m^{-3} (Havelka *et al.* 1984b). Sweet potato had greater cellulose content of stems when grown with 506 rather than 354 $cm^3(CO_2)$ m^{-3} but the contents of hemicellulose in leaves together with lignin in stems decreased (Bhattacharya *et al.* 1988). The tubers contained less protein, total carotenoids and fibre and had a smaller per cent of nitrogen and protein, while water content decreased at high CO_2 (Biswas and Hileman 1985). Bhattacharya *et al.* (1990) observed that sweet potato grown in EC had increased starch content in storage tubers and leaves but not in stems, compared to those grown in AC under both well-watered and droughted conditions (Lawlor and Mitchell 1991). Some empirical relationships between leaf dimensions, leaf area and dry mass hold over a range of CO_2 concentrations in soybean (Lieth *et al.* 1986, Leadley and Reynolds 1988). The simple models relating the effect of CO_2 on yield to water stress of the plant work well for cotton and water hyacinth (Idso *et al.* 1987b), and the response of soybean to EC was used to formulate a model of yield as a function of E, which was used to predict the effects of rising CO_2 on soybean yields (King *et al.* 1985). However, there is insufficient evidence of development and improvement of testing of models to tackle the problem of EC and crop responses using adequate data sets (Lawlor and Mitchell 1991).

A CO_2 enrichment of 675 $\mu mol(CO_2)$ mol^{-1} caused a significant increment of shoot dry mass, whereas no changes were observed in fresh mass, chlorophyll or protein contents in barley. At an irradiance of 860 μmol m^{-2} s^{-1}, CO_2 enrichment caused photosynthetic capacity to increase by 250 %, whereas no effect was observed at 80 μmol m^{-2} s^{-1} (Ingvardsen and Veierskov 1994). Large quantities of starch and/or other nonstructural saccharides accumulate in the leaves and other tissues of plants grown under EC (Bisbal 1987, Allen 1989, Baker *et al.* 1989). Increase in specific leaf mass (mass per unit area) may be due to increased nonstructural saccharides (starch) as well as to increased thickness of leaves (Allen 1989). The presence of large starch grains in the chloroplasts of plants grown at EC was found in tomato (Madsen 1968a) and *Trifolium* (Cave *et al.* 1981). The large amount of starch grains might disturb the function of the thylakoid membrane. The inhibitory effect of photosynthates under EC would agree with the assumption of Caemmerer and Farquhar (1984) that high CO_2 decreases the regenerative capacity of RuBP and RuBPC activity. The link with the accumulation of starch in the chloroplast could be the perturbation of ATP production in thylakoid membranes inhibiting RuBP regeneration (Du Cloux *et al.* 1989). Herbaceous C_3 plants grown in

EC show increases in carbon assimilation and saccharide accumulation (particularly starch) within the source leaves (Baxter *et al.* 1994a,b).

In general, EC results in greater amounts of starch accumulation in leaves (Huber *et al.* 1984a, Bhattacharya *et al.* 1985a, Allen *et al.* 1988, Allen 1989, 1990). Many plants show an increase in leaf starch content on long-term treatment with EC; for example, *Cucurbita pepo* (Brown and Escombe 1902), *C. sativus* (Madore and Grodzinski 1985), *Eichhornia crassipes* (Spencer and Bowes 1986), *Fuchsia* sp. (Brown and Escombe 1902), *G. max* (Cure *et al.* 1987), *Gossypium hirsutum* (Chang 1975), *Impatiens platypetala* (Brown and Escombe 1902), *L. esculentum* (Yelle *et al.* 1989a), *Medicago sativa* (Baysdorfer and Bassham 1985), *Phaseolus sativus* (Hoddinott and Jolliffe 1988), *Plantago major* (Poorter *et al.* 1988), and *Trifolium subterraneum* (Cave *et al.* 1981, Farrar and Williams 1991). Short-term EC also increases the accumulation of starch within the source leaves of *G. max* (Geiger *et al.* 1983, Huber *et al.* 1984a) and *P. vulgaris* (Sharkey *et al.* 1985). Increasing concentrations of CO_2 alter the dual pattern of deposition and mobilization of chloroplast starch. In leaves of tomato under EC the basal leaf starch content was higher and the daily change was greater due to a prolonged duration of starch accumulation during the day (Yelle *et al.* 1989a). However, the major increase in leaf saccharide content observed for the EC C_3 plants is always starch. Indeed, the sucrose:starch ratio of soybean leaves reveals a marked decline with increasing intercellular CO_2 partial pressure (Sharkey *et al.* 1985). With a few exceptions, hexose and sucrose are higher in concentration in leaves following short-term (Geiger *et al.* 1983) or long-term CO_2-enhancement (Yelle *et al.* 1989a, Farrar and Williams 1991).

Crop photosynthesis

In spite of interaction and strong coupling between temperature and irradiance, there is evidence that temperature rather than irradiance determines the high CO_2 modification factor (Nijs *et al.* 1992). Further, EC alleviates the afternoon depression in CO_2 uptake rate observed in AC plants. When comparing long-term EC experiments on plant growth, the CO_2 concentration is generally the primary determinant of the increase in absolute production. A good point of reference in this respect is the 33 % increase in average yield for a doubling of AC resulting from Kimball's (1983) analysis. To adequately predict future plant productivity, expected climatic changes in air temperature, cloud cover, precipitation, *etc.* have to be taken into account, and the effect on plants of interactions between long-term EC and environment becomes important. Special attention is given to the influence of air temperature on the relative stimulation of plant growth by EC, the so-called 'growth modification factor' (Allen *et al.* 1990). For an air temperature increase of 3-4 °C changes in the plant response to EC could be in the order of hundreds of per cent, as calculated by Idso *et al.* (1989). Temperature influence on the CO_2 effect is at present insufficiently characterized, for many individual processes that are affected by increasing CO_2 concentration are at the same time temperature-dependent: *e.g.*,

enzymatic reactions of the reductive C_3 cycle, photorespiration and dark respiration, CO_2 transport and solubility, stomatal response, metabolic activity at the sinks for saccharides, and their feedback mechanisms. Temperature is substantially rate-limiting for enzymatic reactions only under adequate irradiance and minimal CO_2 availability. Campbell *et al.* (1990) measured decreased RuBP levels in the leaves of soybean grown in elevated temperature at both AC and doubled CO_2 concentration, indicating increased substrate use of RuBPCO (Lawlor and Mitchell 1991). Interactive effects of CO_2 and temperature on R_D are uncertain because the respiratory response to CO_2 alone is still poorly understood. Tracking of continuously changing canopy gas exchange rates in AC and EC under the influence of coupled external temperature and irradiance can inform on the environmental dependence of the CO_2 modification factor as well as of its ecophysiological basis (Lawlor and Mitchell 1991).

Only a small proportion of EC studies on crops has been done in the field. CO_2 increases P_N, dry matter production and yield, substantially in C_3 species but less in C_4 ones (Lawlor and Mitchell 1991). It decreases g_s and E in C_3 and C_4 species and greatly improves WUE in all plants. The increased productivity of EC crops is also related to the greater leaf area produced. There is little evidence of a consistent effect of CO_2 on partitioning of dry matter between organs or on their chemical composition, except for tubers. Work has concentrated on a few crops (largely soybean) and more is needed on crops for which there are a few values. Field studies on the effects of EC in combination with temperature, water and nutrition are also essential (Lawlor and Mitchell 1991).

Productivity and source-sink relationship

Due to high CO_2 concentration the soybean yield increased almost entirely as a result of greater numbers of seeds (Rogers *et al.* 1983a, Ackerson *et al.* 1984, Havelka *et al.* 1984a), and this, in turn, was due to an increased number of pods, rather than the number of seeds per pod, which actually decreased (Ackerson *et al.* 1984, Lawlor and Mitchell 1991). In bean (*Phaseolus vulgaris*), the EC increased the number of pods, decreased the number of seeds per pod but did not affect mean seed mass (Gustafson 1984). In rice, the number of panicles per plant was almost entirely responsible for a 47 % increase in grain yield due to a doubling of CO_2 (Baker *et al.* 1990). In wheat, increases in yield with EC were again due to increases in the number of grains, rather than in grain mass (Fischer and Aguilar 1976) due to a greater number of ears (Havelka *et al.* 1984b). Sweet potato yields also increased entirely as a result of more tubers rather than of mass per tuber (Biswas and Hileman 1985, Lawlor and Mitchell 1991).

The effect of EC on yield is dependent on the stage of growth at which it is applied. Enrichment from emergence to anthesis or from anthesis to early pod development did not increase soybean yield, while enrichment from early pod development until maturity and from emergence to maturity increased yields by 27 and 36 %, respectively (Ackerson *et al.* 1984). These findings suggest that the

additional saccharides formed with enrichment are required during early flower and seed development. The lack of understanding of factors determining the distribution of saccharides and nitrogenous compounds into sinks precludes prediction of the effects of enrichment under a range of conditions (Lawlor and Mitchell 1991).

Accumulation of saccharides within leaves of the EC plants may reflect a temporary or permanent imbalance between sources and sinks and may help to explain the contradictory reports of increased assimilate export (Farrar and Williams 1991). Manipulation of the source:sink ratio in both soybean and tomato plants by leaf pod or fruit removal (Ito 1973, Clough *et al.* 1981, Peet 1984) alters the rate of photosynthesis of source leaves. Plants with a low source:sink ratio (limiting leaf number) increase P_N more than plants with a high source:sink ratio (limiting pod or fruit number) whether in AC or EC. A negative correlation between starch content and P_N exists for the EC plants (Ehret and Jolliffe 1985) and under extreme starch accumulation damage to the thylakoid system may occur (Madsen 1975, Carmi and Shomer 1979). Direct inhibition by starch of P_N is unlikely (Yelle *et al.* 1989b). Whether the capacity of sinks to grow is sufficient to maintain elevated P_N is a general argument in whole-plant partitioning (Farrar and Williams 1991). A marked increase in the rate of assimilate accumulation by the EC plants occurred over the first 3 d but was not maintained being offset by increased rates of assimilate utilization initially in the dark and later in the light. Cure *et al.* (1987) propose an increase in assimilate export within the EC plants. Rogers *et al.* (1982) reported an increase in pod number of 'Bragg' soybeans grown under two water regimes with EC. Bhattacharya *et al.* (1985b) also reported an enhanced vegetative and reproductive growth of cowpeas grown at EC under controlled environment. The EC increased the number but not the individual mass of seeds. Allen *et al.* (1987) used a modified Michaelis-Menten type of model to express relative P_N, biomass yield and seed yields of soybean, as a function of CO_2 concentration from several years of measurement at several locations (Table 2). This increase in yield was only observed when EC was applied from emergence to maturity or from early podfill to maturity (Ackerson *et al.* 1984). Prior to flowering, the EC plants accumulated more leaf starch, sucrose and glucose which were then rapidly depleted to support the increased sink growth of the seed pods. Such leaves still contained more leaf starch at maturity than plants grown at AC; hence not all of the saccharide reserves are used for sink growth indicating an inefficient utilization of assimilate or feed-back from the sink. The harvest index of both wheat and soybean remained constant with increasing CO_2 (Pearcy and Björkman 1983, Ackerson *et al.* 1984, Farrar and Williams 1991).

Table 2. Soybean responses to rising CO_2 predicted by the nonlinear, hyperbolic modified Michaelis-Menten model. From Allen *et al.* (1987).

Assumed period	CO_2 change [μmol mol^{-1}]	Increase [%] in photosynthesis	biomass	seed amount
1800-1958	276-315	12	10	8
1800-1986	276-345	20	17	13
1958-2058	315-630	53	43	32

Leaf enzymatic responses to CO_2 enrichment

The possible effects of AC on several plant C-metabolism processes have been reviewed by Tolbert and Zelitch (1983). Recent research has been conducted mainly on two enzymes in C_3 plants, RuBPCO (Vu *et al.* 1983, Grob *et al.* 1993) and SPS (Huber 1983), and on PEPC in C_4 plants (Simon *et al.* 1984, Grob *et al.* 1993). However, the RuBPC activity of older leaves showed smaller differences. The RuBP concentrations were about 30-50 % higher for leaves of soybean plants grown at 800 than 330 μmol(CO_2) mol^{-1}. There was little difference in soybean leaf RuBPCO activity on a leaf-area basis or soluble protein basis of plants grown at CO_2 concentration from 160 to 990 μmol mol^{-1} (Campbell *et al.* 1988). However, the RuBPCO activity on a dry mass basis decreased across those respective CO_2 concentrations, presumably because of increased SLM attributable to increased leaf thickness and increased storage of starch (Thomas and Harvey 1983, Vu *et al.* 1989). Campbell *et al.* (1988) also showed that soybean RuBPCO protein was a constant fraction (about 55 %) of total soluble protein regardless of CO_2 treatments. In contrast to the findings of Vu *et al.* (1983), Campbell *et al.* (1988) found that RuBP concentrations in soybean leaves tended to decrease with increasing CO_2 (Allen 1990).

No differences were found in RuBPC activities of wheat leaves when expressed on a leaf-area basis (Havelka *et al.* 1984a). The RuBPC activity in *Nerium oleander* was reduced significantly at 660 μmol(CO_2) mol^{-1} with respect to 330 μmol mol^{-1} when expressed on the basis of soluble protein (0.75) but the reduction was not statistically significant when expressed on a per-unit leaf-area basis (0.95) or chlorophyll basis (0.91) (Downton *et al.* 1980). In conclusion, EC raises the substrate RuBP slightly but reduces slightly also the *in vitro* activity of the RuBPC. However, neither of these responses is the primary cause of increased leaf P_N at EC (Allen 1990).

The effect of EC on the activities of enzymes associated with assimilate partitioning is largely unknown (Farrar and Williams 1991). The SPS is a key enzyme in rate-control of sucrose synthesis (Huber *et al.* 1986), the activity of SPS in a variety of species being negatively correlated with leaf starch accumulation (Huber *et al.* 1984a,b, Farrar and Williams 1991).

Short-term treatment of soybean plants with EC doubled the starch content and decreased the activity of SPS within the leaves (Huber *et al.* 1984a,b). Short-term treatment of plants with EC increases leaf starch content at the expense of export of assimilates from the leaf. This negative correlation between SPS activity and starch accumulation for EC plants has also been observed for leaves of *C. sativus* (Peet *et al.* 1986). In contrast, the SPS activity of rice leaves at 660 cm^3(CO_2) m^{-3} increases two- to three-fold when compared with the control (Hussain *et al.* 1990, Farrar and Williams 1991).

CO_2-dependent increases of P_N of high- and low-RuBPCO plants virtually disappeared after 9 d of growth in an EC chamber (Sicher *et al.* 1994). Total above-ground dry matter production of high- and low-RuBPCO plants was 28 and 53 % greater, respectively, after 9 d of growth at 70 compared with 35 Pa CO_2. Most of

this dry mass gain was due to increased SLM. The RuBPCO activity, RuBPCO protein and total chlorophyll contents were lower in both high- and low-RuBPCO plants grown in EC compared with AC. Soluble leaf protein content also decreased in response to EC in high, but not in low-RuBPCO tobacco plants. Decreased RuBPCO activity in CO_2-adapted high- and low-RuBPCO plants was not attributable to changes in activation state of the enzyme (Sicher *et al.* 1994). Carbonic anhydrase activities and subunit concentrations measured with specific antibodies were similar in high- and low-RuBPCO tobacco plants and were unchanged by CO_2 enrichment. Collectively, these findings suggested that photosynthetic acclimation to EC occurred in tobacco plants either with or without transgenically decreased RuBPCO concentrations and also indicated that the down-regulation of RuBPCO in CO_2-adapted tobacco plants was related to decreased specific activity of this enzyme (Sicher *et al.* 1994).

Acclimation to EC usually results in a down regulation of CO_2 fixation, although long-term positive changes in carbon assimilation rate also have been reported (*e.g.*, Campbell *et al.* 1990, Ziska *et al.* 1990). Photosynthetic adjustment varies within the same species (Clough *et al.* 1981, Campbell *et al.* 1990, Bunce 1992). It is not possible to predict long-term effects of EC on plant growth and development without an improved understanding of the underlying mechanisms of photosynthetic acclimation (Sicher *et al.* 1994). Biochemical factors that induce photosynthetic acclimation during plant growth in EC are poorly understood. The RuBPCO activity was decreased in species exhibiting negative photosynthetic acclimation (Wong 1979, Peet *et al.* 1986, Sage *et al.* 1989, Yelle *et al.* 1989b, Sicher *et al.* 1994).

Transgenic plants offer a novel approach to the study of photosynthetic metabolism and the physiological responses of plants to environmental change (Sonnewald and Willmitzer 1992, Vivekanandan and Saralabai 1994). Rodermel *et al.* (1988) genetically transformed tobacco plants with antisense DNA sequences to *rbcS*. The transformants synthesized mRNA in the antisense orientation and exhibited decreased RuBPCO protein and activity (Sicher *et al.* 1994). The transformed plants had altered photosynthetic properties, although under some conditions up to 50 % of the RuBPCO could be removed from the leaf without affecting P_N (Stitt *et al.* 1991).

Photorespiration

Oxygen in the chloroplasts can interfere with the photosynthetic reduction of CO_2. As CO_2 concentration increases, CO_2 would more likely than oxygen bind to the active site of RuBPC because more CO_2 molecules would be present there. Indeed, in some experiments photorespiration was reduced by 50 % when CO_2 concentrations increased to 600 cm^3 m^{-3}. Limiting photorespiration means that plants can use more of their energy to build tissues (Bazzaz and Fajer 1992).

Respiration

High canopy R_D in the EC (631±43 cm^3 m^{-3}) treatment can be partly attributed to a large number of respiring plant parts and possibly also to high leaf R_D that sometimes accompanies increased growth rate (Ceulemans 1980, Nijs *et al.* 1989b). Oxygen uptake was reduced by 40 % by the EC treatment, but the EC plants were similar to the AC plants when returned to the AC conditions. The R_D is governed by both the saccharide status and adenylate supply, and the sucrose content of the tissue dictates the capacity of mitochondrial respiration. The R_D of growing plant tissue is stoichiometrically linked to its rate of growth (Farrar and Williams 1990). One would expect at least transient increases in respiration rate for those parts of a plant that show increased growth and assimilate accumulation under EC, *i.e.*, source leaves, individual sink tissue (fruit, seed, stem, roots, *etc.*). Long-term treatments with EC result in a decline in whole-plant respiration (Bunce 1990, Farrar and Williams 1991).

Bunce and Caulfield (1991) reported that in *Dactylis glomerata*, relative growth rate was 50 % higher at EC than at AC. Also the respiratory CO_2 efflux was reduced at EC. The R_D was decreased with increased CO_2 pressure in the range of 0-100 Pa (Reuveni and Gale 1985, Bunce 1990). Reduction in R_D at EC in spite of increased growth may indicate that some respiration is unnecessary and could profitably be eliminated from plants in current environments (Gifford *et al.* 1985, Reuveni and Gale 1985). Plants at EC either have a higher growth conversion efficiency or lower maintenance respiration. Reuveni and Gale (1985) reported a larger relative decrease in CO_2 efflux in plants exposed to EC at night when R_D was measured after prolonged darkness, which might indicate that maintenance respiration was reduced. Bunce and Caulfield (1991) reported that EC decreased whole plant dark CO_2 efflux in a way which was superficially incompatible with the growth and maintenance model of respiration. They also reported that the physiological significance of the inhibition of whole plant CO_2 efflux by EC depends on what mechanism(s) is, in fact, operating. Their field results indicated equal or less CO_2 efflux at EC, along with a greater harvested mass, thus indicating reduced CO_2 efflux per unit of biomass accumulated at elevated EC (Bunce and Caulfield 1991).

Nutrition quality and insect population

Changes in the nutrition quality of plant leaves could lower herbivore and predator populations within their habitats. The amount of nitrogen and hence protein in plant leaves determines the growth and fecundity of insect herbivores. Bazzaz and Fajer (1992) suggested that insect herbivore performance and subsequent population size may be decreased on such a diet. On a plantain grown in an EC environment, larvae of the butterfly *Junonia coenia* did not develop as rapidly and died more frequently. Slower larval growth can mean that fewer individuals reach adulthood, because caterpillars remain vulnerable to attack from predators and parasites. If insect

herbivores suffer population reductions in a world abundant with carbon dioxide, many predators will have less prey (Bazzaz and Fajer 1992).

Conclusions

The CO_2-irradiance interaction is equally influential on P_N. In addition, empirical evidence now suggests that an increase in air temperature may be associated with general increase in cloud cover. Predictions of the "greenhouse effect" on cloud cover are necessary before an impact on photosynthesis and plant growth can be accurately predicted (Allen *et al.* 1990). The association between plants and root symbionts such as nitrogen-fixing bacteria and mycorrhizal fungi may be enhanced in the future. The CO_2 fertilization effect does not guarantee a lush, green future of agricultural abundance (Mo *et al.* 1992). The increased CO_2 stimulates total dry matter production and yield by increasing P_N and leaf area growth. The increase in yield is achieved largely by increasing the number of tillers or branches in mono- and dicotyledons, and hence the number of seed and grain, and tubers in root crops; this increases storage sites (Lawlor and Mitchell 1991). The limited information suggests that quality of products is relatively unaffected. The CO_2 enrichment decreases the g_s and E, although increasing leaf temperature together with greater LAI offsets the advantage accrued by smaller g_s. However, WUE generally increases. Lawlor and Mitchell (1991) suggest the following lacunae in our understanding of the effects of EC on plants: (*1*) Experimental field values for the effects of EC in combination with temperature, nutrition and water supply are under-represented in the literature compared with controlled-environment studies. Therefore, it is imperative to address field conditions. (*2*) There is a large species imbalance in the results, with soybean well represented, cotton less so, and totally inadequate information for all other crops, particularly cereals (wheat, barley and *Sorghum*) and tuber crops. Programmes concentrating on key economically important crops are vital. (*3*) Field studies need to be closely linked with mechanistic modelling, so that specific predictions can be tested and the areas in greatest need of further research identified. Thus, modelling expertise should be combined. (*4*) The responses to the environment of different genotypes of the same crop, with well established genetically determined characteristics, have not been adequately analysed; they should be addressed if crops are to be optimized to future climates. (*5*) The different methods of enriching crops with CO_2 in the field have relative advantages which must be considered in conjunction with the costs. Although expensive, free-air enrichment is the best approach for gathering relevant data for assessing the impact of EC on crops, while open-top chambers are more amenable to the study of interactions with temperature and other related parameters.

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biologia plantarum

CONTENTS 38 (4): 481-640, 1996

Cytokinins in the hemiparasite *Melampyrum arvense* L. before and after attachment to the host
Z. LECHOWSKI, J. BIAŁCZYK 481-488

Abscisic acid content in the root hemiparasite *Melampyrum arvense* L. before and after attachment to the host plant
Z. LECHOWSKI 489-494

Electrogenic K^+/H^+ exchange in excised wheat roots
V. PAKHOMOVA 495-499

Effect of short-term heat treatment of rice seedlings on sensitivity of thylakoid membranes to photoinhibition
B. VANI, P. PARDHA SARADHI, PRASANNA MOHANTY 501-509

Seasonal changes in sugar beet photosynthesis as affected by exogenous cytokinin N^6-(*m*-hydroxybenzyl)adenosine
J. ČATSKÝ, J. POSPÍŠILOVÁ, M. KAMÍNEK, A. GAUDINOVÁ, J. PULKRÁBEK, J. ZAHRADNÍČEK .. 511-518

Soil salinity effects on transpiration and net photosynthetic rates, stomatal conductance and Na^+ and Cl^- contents in durum wheat
S.K. SHARMA 519-523

Effect of sodim and calcium chlorides, abscisic acid and proline on callus cultures of *Arachis hypogaea* L.
A. GUPTA, G.S. SINGHAL 525-529

Growth and proline accumulation in mungbean seedlings as affected by sodium chloride
A.N. MISRA, B. MURMU, P. SINGH, M. MISRA 531-536

Growth, nodulation and nitrogen fixation in soybean as affected by air humidity and root temperature
J. STOYANOVA 537-544

Natural and dark-induced nodule senescence in chickpea: nodule functioning and H_2O_2 scavenging enzymes
S. SHEOKAND, K. SWARAJ 545-554

Induction of sister chromatid exchanges by heavy metal salts in root meristem cells of *Allium cepa* L.
K.K. PANDA, J. PATRA, B.B. PANDA 555-561

Effect of pH, irradiance and population size on the toxicity of *Furadan* to two species of *Anabaena*
B. RATH, S.P. ADHIKARY 563-570

Distribution of the stress-related anionic peroxidases in different cucumber organs
V. REPKA, I. FISCHEROVÁ 571-583

Expression of cucumber stress-related anionic peroxidases during flower development or a cryptic infective process
V. REPKA, I. FISCHEROVÁ, K. ČANIGOVÁ 585-596

The level of proteins and leakage of solutes in germinating fresh and stored seeds of *Cicer arietinum* L.
S. HAYAT, A. AHMAD 597-599

Effect of gibberellic acid and nitrogen on carbonic anhydrase activity and mustard biomass
N.A. KHAN, H.R. ANSARI, M. MOBIN 601-603

Hardening by abscisic acid of tobacco plantlets grown *in vitro*
J. POSPÍŠILOVÁ 605-609

Soil salinity effect on soluble saccharides, phenol, fatty acid and mineral contents, and respiration rate of garlic cultivars
S. SIDDIQUI, K. GUPTA, A. YADAV, J.L. MANGAL 611-615

Endogenous indole-3-acetic acid during adventitious root formation in *Populus* × *canadensis* Moench.
T. DOLEŽELOVÁ, V. PSOTA, Z. FEIGLOVÁ 617-619

Chlorophylls and carotenoids in calli of sugar beet genotypes
B. KRSTIĆ, S. MEZEI, L. KOVAČEV, S. PAJEVIĆ 621-624

Chlorophyll fluorescence and anthocyanin content in chilled maize plants after return to a non-chilling temperature under various irradiances
T. JANDA, G. SZALAI, E. PÁLDI 625-627

Water relations and nitrogen fixation in potassium fed *Vigna radiata* nodules
A.S. NANDWAL, B.S. KUNDU, A. HOODA, M.S. KUHAD 629-632

Protein and chlorophyll contents in autotrophically and heterotrophically cultivated tobacco mesophyll protoplasts
M. ŠINDELÁŘOVÁ, L. BURKETOVÁ, L. ŠINDELÁŘ 633-635

Effect of formaldehyde and glutaraldehyde fixation on the immunochemical reactivity of potato virus A with monoclonal antibodies
T. MORAVEC, N. ČEŘOVSKÁ 637-640