Open Top Chambers used for assessment of the response of wheat (C_3) and maize (C_4) plants to atmospheric carbon dioxide enrichment. (Photograph J. Rozema).

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Plant responses to atmospheric carbon dioxide enrichment: interactions with some soil and atmospheric conditions

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Abstract

In general, C_3 plant species are more responsive to atmospheric carbon dioxide (CO_2) enrichment than C_4-plants. Increased relative growth rate at elevated CO_2 primarily relates to increased Net Assimilation Rate (NAR), and enhancement of net photosynthesis and reduced photorespiration. Transpiration and stomatal conductance decrease with elevated CO_2, water use efficiency and shoot water potential increase, particularly in plants grown at high soil salinity. Leaf area per plant and leaf area per leaf may increase in an early growth stage with increased CO_2, after a period of time Leaf Area Ratio (LAR) and Specific Leaf Area (SLA) generally decrease. Starch may accumulate with time in leaves grown at elevated CO_2. Plants grown under salt stress with increased (dark) respiration as a sink for photosynthates, may not show such acclimation to increased atmospheric CO_2 levels. Plant growth may be stimulated by atmospheric carbon dioxide enrichment and reduced by enhanced UV-B radiation but the limited data available on the effect of combined elevated CO_2 and ultraviolet B (280–320 nm) (UV-B) radiation allow no general conclusion. CO_2-induced increase of growth rate can be markedly modified at elevated UV-B radiation. Plant responses to elevated atmospheric CO_2 and other environmental factors such as soil salinity and UV-B tend to be species-specific, because plant species differ in sensitivity to salinity and UV-B radiation, as well as to other environmental stress factors (drought, nutrient deficiency). Therefore, the effects of joint elevated atmospheric CO_2 and increased soil salinity or elevated CO_2 and enhanced UV-B to plants are physiologically complex.

Introduction

Plant primary production depends on many factors including the physiology and morphology of the plants, and environmental factors, such as irradiance, temperature, water and nutrient availability. For C_3-plants, representing more than 95% of all plant species in the world (Houghton *et al.* 1990), atmospheric CO_2 enrichment will lead to significantly increased net photosynthesis, caused by an increased ratio of CO_2 and O_2 at the catalytic site on Rubisco (ribulose biphosphate carboxylase oxygenase) and decreased diffusion limitation (Kimball 1985). In C_4-plants, this effect will be less marked because phosphoenol pyruvate carboxylase catalyses the photosynthetic fixation of CO_2 in mesophyll cells and this eventually causes a high ratio of CO_2 and O_2 in the bundle sheath cells, where carboxylation occurs once more (Allen 1990).

Information on the interaction of CO_2 and other environmental factors is scanty (Kimball

1985). Among the environmental factors that are likely to interact with the effect of carbon dioxide enrichment are: temperature, irradiation (including ultraviolet B radiation), nutrient availability, drought humidity, and pollutants in the air. In a review of plant responses to rising CO_2 and interactions with air pollutants Allen (1990) speculated on a reduction of effects of O_3 and SO_2 with elevated atmospheric CO_2 as a result of decreased stomatal conductance. However, research confirming this hypothesis is lacking. From the analysis of growth (cf. Lambers *et al.* 1990) it can be seen that increased growth rate with carbon dioxide enrichment can be primarily attributed to an increase of NAR, the 'physiological' component and maybe to an increase of LAR, the 'morphological' component. There is increasing evidence that growth stimulation by elevated CO_2 is primarily due to increased carboxylation and reduced photorespiration (Warrick *et al.* 1986). Changes in the allocation of dry matter between plant organs, such as changes in the root/shoot ratio and the Leaf Weight Ratio (LWR) have not been found (den Hertog *et al.* 1992, this volume, this paper, Stulen & den Hertog 1992, this volume). When the interaction of CO_2 enrichment with soil salinity is considered, no changes of LWR and R/S ratio have been detected (Lenssen *et al.* 1992, this volume). Here, an attempt is made to summarize interactive effects of CO_2 enrichment, salinity and enhanced UV-B radiation on plants.

Studies of plant responses to increased CO_2 have demonstrated that an increased rate of net photosynthesis may be transient in CO_2 enrichment studies (Eamus & Jarvis 1989). Such acclimation may occur when Rubisco levels are reduced or when carbohydrate accumulation causes feedback inhibition of the carboxylating enzyme (Bazzaz 1990). Since plant growth and plant primary production may be limited by numerous physiological and environmental factors, many interactive effects may occur as well (Kimball 1985). Among these physiological and environmental factors are different CO_2 fixation pathways (C_3, C_4 and CAM), temperature, nutrient and water availability, irradiance and air pollution and pests and plant diseases. In recent publications (Kimball 1985; Eamus & Jarvis 1989; Krupa & Kickert 1989; Krupa & Kickert 1992, this volume; Allen 1990) plant responses to rising carbon dioxide and various interactions with environmental factors such as air pollution, have been discussed. Carbon dioxide enrichment may stimulate net photosynthesis of C_3 plants, but relatively little or no stimulation in C_4 plants (Strain & Cure 1985). Transpiration in C_3 plants may be reduced with elevated atmospheric CO_2 as a result of (partial) stomatal closure (Morison & Gifford 1983). As a result, the water potential of the shoots may be markedly increased (Table 1) (cf. Sionit *et al.* 1985; Wray & Strain 1985). The results shown in Table 1 do not indicate reduced transpiration and increased shoot water potential in the C_4 cereal crop, maize. Reduced transpiration and increased shoot water potential with elevated CO_2 have been reported for the C_4 plant *Spartina patens* (Curtis *et al.* 1989a and b; Rozema *et al.* 1991). In this review, the interaction of atmospheric carbon dioxide enrichment with atmospheric conditions such as temperature and irradiance (enhanced UV-B) and some soil factors such as water stress (drought and salinity) and flooding will be discussed in more detail. Attention will be focussed on the analysis of growth and the various growth parameters (cf. Lambers

Table 1. Rate of net photosynthesis and transpiration of single leaves of wheat (*Triticum aestivum* cv Obelisk) and maize (*Zea mays* cv. LG5) and water potential (MPa) of the shoot (measured with Scholander's pressure bomb at midday) with ambient and elevated atmospheric CO_2. Average values of four replicates with standard error of the mean.

		CO_2 μmol mol^{-1}	
		350	760
Net photosynthesis μmol CO_2 m^{-2} s^{-1}	Wheat	7.8 ± 3.2	14.9 ± 3.4
	Maize	21.3 ± 2.0	19.0 ± 3.1
Transpiration rate mmol H_2O m^{-2} s^{-1}	Wheat	16.4 ± 1.9	13.9 ± 1.7
	Maize	4.8 ± 0.5	4.7 ± 0.8
Waterpotential MPa	Wheat	-1.53 ± 0.17	-0.79 ± 0.10
	Maize	-0.78 ± 0.29	-0.81 ± 0.18

et al. 1990) in response to rising carbon dioxide and environmental factors. Growth reduction occurs with increased salinity and UV-B, but it has been suggested, that CO_2 enrichment may counteract or alleviate this reduction. This review considers evidence for this hypothesis.

CO_2 enrichment and temperature

Idso *et al.* (1987) studied the response of many plant species to increased atmospheric CO_2 under various temperature regimes and concluded that plant growth response to increased CO_2 was greater at higher temperature. There may be no or even a negative response from plants, to elevated CO_2 at temperatures below 18.5 °C.

Plants from different climate zones and plants adapted to different seasons within a climate zone demonstrate a large range of temperature preferences with regard to growth, photosynthesis, respiration and germination. Obviously, a change in temperature of 1.5–4 °C, as predicted for global warming, will have different effects on plants originating from arid regions or those from the cold tundra.

Generally speaking under the current environmental conditions C_4 plants have a higher temperature optimum for photosynthesis than co-occurring C_3 plant species (De Jong *et al.* 1982; Drake 1989). Analysis of the effects of the interaction of temperature and atmospheric CO_2 is important for various reasons. Firstly, marked spatial and temporal variation in temperature exists over the earth. Atmospheric CO_2 enrichment will lead to increased growth of many species, but this effect is dependent on temperature (Baker *et al.* 1989). Therefore, a global assessment of the effects of CO_2 increase on (agro)ecosystems and vegetation requires careful analysis of the interaction between CO_2 enrichment and temperature (cf. Goudriaan *et al.* 1990; Goudriaan & Unsworth 1990). Secondly, climatic change comprises the simultaneous increase in atmospheric CO_2 and perhaps global warming. By the year 2050, a doubling of the pre-industrial atmospheric CO_2 is expected, reaching to about 560 μmol-mol^{-1} CO_2 and by then, the mean global temperature may have risen by 1.5–4.0 °C (Houghton *et al.* 1990). This will differentially affect the response of C_3 and C_4 plants, as well as the ecosystem as a whole (Bazzaz 1990).

Although some modelling reports on the joint effects of CO_2 enrichment and global warming are available (Goudriaan *et al.* 1990) experimental data are remarkably scarce. Not only will photosynthesis and respiration be affected by change of temperature, but many other metabolic processes in plants are temperature dependent as well (Warrick *et al.* 1986; Campbell *et al.* 1990; Baker *et al.* 1989).

We conducted an Open Top Chamber experiment in the autumn of 1990, in Amsterdam, with wheat and maize cultivated in pots filled with garden soil and the exposure treatments consisted of ambient (350 μmol mol^{-1} CO_2) and elevated (700 μmol mol^{-1} CO_2) carbon dioxide levels. Photosynthesis in wheat increased at elevated CO_2, transpiration decreased in both wheat and maize, yet, there was no significant effect of CO_2 enrichment on the biomass of both plant species. It is hypothesized that the relatively low daytime temperatures during the autumn (10–14 °C) inhibited the transport and conversion of photosynthates. Alternatively it can be expected that increased photorespiration at a higher temperature leads to an enhanced effect to atmospheric CO_2 enrichment.

C_3-plants may be more favoured by atmospheric CO_2 enrichment and C_4 plants more by global warming. C_3 plants occur in a range of climatic zones varying in temperature, $CO_2 \times$ temperature interaction will probably be highly species specific. It is therefore uncertain what predictions can be made for plant responses to simultaneous increases in atmospheric CO_2 and global temperature.

CO_2 enrichment and irradiance

Carbon dioxide enrichment increases the growth rate of many plants at low light intensity, but C_3 and C_4 plants could be expected to differ in their response. In C_3 plants (but not in C_4 plants) CO_2 enrichment will suppress photorespiration. As a result the quantum yield of leaf photosynthesis increases at elevated CO_2 (Pearcy & Björkman 1983; Warrick *et al.* 1986). For some species, for example, for wheat the relative increase in growth rate due to elevated CO_2 is higher at low light intensities (Sionit *et al.* 1982). For other C_3 plants the growth response to carbon dioxide enrichment does not differ between low and high light intensities (Sionit *et al.* 1982; Kendall *et al.* 1985a and b). Kimball (1985) concludes 'that by the time a plant has integrated its varying photosynthetic response into a final growth response, the stimulation of C_3 crops by CO_2 enrichment is roughly the same over a very wide range of light regimes'.

It is therefore unlikely to expect that plant responses to CO_2 enrichment will strongly depend on variation of levels in the irradiance.

CO_2 enrichment and UV-B radiation

Global climatic change, among other things comprises rising levels of atmospheric carbon dioxide, predominantly the result of combustion of fossil fuels, and enhanced levels of UV-B radiation due to stratospheric ozone depletion (Houghton *et al.* 1990; Rozema *et al.* 1991c). Atmospheric carbon dioxide and solar ultraviolet-B (UV-B-between 280–320 nm) will rise simultaneously. Despite numerous ecophysiological studies on the individual effects of CO_2 and UV-B radiation on plants and ecosystems, there are only few studies, on the combined effects of increased atmospheric CO_2 and enhanced UV-B on plants (cf. Krupa & Kickert 1989). Atmospheric carbon dioxide enrichment tends to increase the rate of net photosynthesis of C_3 plants and reduce stomatal conductance (Allen 1990). As discussed before, the growth of many plants increases with elevated atmospheric CO_2. Growth of most species is reduced by elevated UV-B, but some are not affected (Teramura 1987). Plant species differ markedly in sensitivity to enhanced UV-B radiation (Teramura *et al.* 1990). Although some reports refer to field experiments, much work on effects of elevated UV-B on plants is based on studies in controlled environments.

Rozema *et al.* (1990b) reported on the combined effect of increased carbon dioxide and UV-B radiation on pea (*Pisum sativum*), tomato (*Lycopersicon esculentum*) and aster (*Aster tripolium*) in a greenhouse experiment. There was a significant increase in the shoot weight of peas and tomatos with elevated carbon dioxide but not in the case of aster. The shoot weights of all three plant species tested, decreased significantly with elevated UV-B radiation (0–2.8 $W \cdot m^{-2}$). This UV-B radiation treatment 0 $W \cdot m^{-2}$ (control) –2.8 $W \cdot m^{-2}$ (elevated) UV-B relates to 40–50% ozone depletion under clear sky. The reduction of shoot weight with increased UV-B was most pronounced in pea, less so in the tomato, and aster was least affected. However, there was no difference in the UV-B induced growth reduction at low (350 $\mu mol\ mol^{-1}$) and high (750 $\mu mol\ mol^{-1}$) CO_2 in the greenhouse. This means that under the experimental conditions used, (175 $\mu mol\ m^{-2}\ s^{-1}$ PAR, 24 °C day/18 °C night, 70% humidity, plants grown in pots filled with garden soil), no statistically significant interaction between the effect of carbon dioxide enrichment and enhanced UV-B radiation could be demonstrated. Yet for the two species which were not sensitive to enhanced UV-B, the growth reduction induced by UV-B was less under elevated CO_2 (Table 2). Teramura *et al.* (1990) reported on the combined effect of elevated UV-B and CO_2 on the productivity and photosynthetic characteristics of wheat, rice and soybean. With increased levels of both CO_2 and UV-B radiation, seed yields and total biomass of wheat and rice did not significantly differ from the control. With soybean CO_2 induced increase in biomass was maintained or even improved with elevated UV-B radiation. This is remarkable, since soybean is reported to be relatively sensitive to enhanced UV-B radiation (Teramura 1987). The statistical analysis performed by Teramura *et al.* (1990) on the biomass data did not aim at an assessment of significance of the interaction of CO_2 enrichment and elevated UV-B radiation. The authors con-

Table 2. Overview of the combined effects of atmospheric CO_2 enrichment and enhanced ultraviolet-B radiation on various plant species.

Plant species	CO_2 treatment (μmol mol^{-1}) ambient-elevated	UV-B levels	Tolerance to enhanced UV-B	Percentage increase in plant biomass with				Comments	References
				CO_2 enrichment		Enhanced UV-B			
				Low	High	Ambient	Elevated		
Pisum sativum	350–760	0–2.8 W m^{-2}	Low	+ 39	+ 27	− 87	− 87	Greenhouse experiment 0–2.8 W m^{-2} (0–22.5 kJ m^{-2} day^{-1}) increase of UV-B radiation relates to 40–50% ozone depletion under clear sky	Rozema *et al.* 1990
Lycopersicon esculentum	350–760	0–2.8 W m^{-2}	Intermediate	+ 42	+ 25	− 28	− 36		
Aster tripolium	350–760	0–2.8 W m^{-2}	High	− 2	+ 4	− 16	− 12		
Triticum aestivum	350–650	8.8–15.7 kJ m^{-2}	Intermediate	+ 65	+ 35	+ 1	− 17	Greenhouse experiment 8.8–15.7 kJ m^{-2} (daily) biolocally effective UV-B relates to 10% ozone depletion under clear sky	Teramura *et al.* 1990
Oryza sativa	350–650	8.8–15.7 kJ m^{-2}	Intermediate	+ 10	+ 9	− 3	− 5		
Glycine max	350–650	8.8–15.7 kJ m^{-2}	Low	+ 15	+ 32	− 5	+ 10		
Elymus athericus	380–720	1–2 W m^{-2}	Intermediate	+ 64	+ 34	− 31	+ 44	Greenhouse experiment 1–2 W m^{-2} increase (10 kJ m^{-2}–16.8 kJ m^{-2} daily biologically effective UV-B) relates to 20% ozone depletion under clear sky	van de Staaij *et al.* 1992

cluded that these results illustrate that increased UV-B radiation may modify CO_2-induced increases in biomass, seed yield and photosynthetic parameters and suggest that available data may not adequately characterize the potential effect of future, simultaneous changes in CO_2 concentration and UV-B radiation (cf. Table 2).

Van de Staay *et al.* (1992, this volume) studied the response of the C_3-salt marsh grass species *Elymus athericus* (= *pycnanthus*) to combined effects of elevated CO_2 and UV-B. In this study plants were grown at two levels of UV-B radiation: $1\,W \cdot m^{-2}$ (control) and $2\,W \cdot m^{-2}$ (enhanced). The difference between these two levels of UV-B radiation relates to 20% stratospheric ozone depletion. *Elymus athericus* showed improved growth with elevated CO_2 and reduced growth under increased UV-B radiation, although there was no statistically significant interaction of CO_2 and UV-B on the plant dry weight. In an analysis of growth the impact of CO_2 enrichment and enhanced UV-B singly and in combination was assessed for all growth parameters. Although there were many significant effects of CO_2 and UV-B as separate factors on growth parameters such as Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Leaf Area Ratio (LAR), Specific Leaf Area (SLA) and leaf area, there was no significance for the interaction of CO_2 and UV-B treatments on any of these growth parameters. The analysis of growth of *Elymus athericus* showed increased NAR with elevated CO_2 and reduced NAR with elevated UV-B. The Leaf Weight Ratio was not changed by CO_2 and UV-B, and the LAR was only slightly affected by the CO_2 and UV-B treatments (Rozema *et al.*, Teramura *et al.* 1990; van de Staaij *et al.* 1992, this volume). Leaf area per plant increased with elevated CO_2 but decreased with enhance UV-B.

Studies of the effects of elevated UV-B radiation due to stratosperic ozone depletion require a careful methodology. In the greenhouse experiments of Rozema *et al.* 1990 and van de Staay *et al.* 1992 levels of elevated UV-B radiation have been rather high in terms of percentage stratospheric ozone depletion. In addition, in UV-B studies performed in the greenhouse with relatively low levels of photosynthetically active radiation, photo-repair may occur much less in comparison with UV-B experiments under field conditions. Overestimation of damage and growth reduction due to UV-B radiation as occurring in greenhouse experiments, will not occur in field experiments with UV-B radiation added to solar UV-B and at high levels of photosynthetically active radiation.

With only three experimental studies available on the combined effect of elevated CO_2 and UV-B no generalizations can be made. However, physiological interactions may be expected. For example, carbon dioxide enrichment stimulates net photosynthesis of many C_3 species, which may lead to an increase in the net assimilation rate (NAR) (Teramura 1987). Disturbance of the photosynthetic electron transport processes, PSII and damage to photosynthetic pigments by enhanced UV-B (Teramura 1987) may result in a reduced net assimilation rate. Damage of the photosynthetic apparatus by UV-B radiation may reduce or prevent the carboxylation response of plants to increased CO_2. In this case a negative interaction between elevated CO_2 and UV-B may occur. Enhanced UV-B radiation may also disrupt stomatal opening (Teramura 1987). If this affects transpiration rate and photosynthesis, interaction with CO_2 enrichment may also be expected. More generally, it may be expected that plants growing in an environment with increased UV-B radiation, will be more sensitive to abiotic (e.g. water, nutrient) and biotic (e.g. pathogens) environmental stresses (Krupa & Kickert 1989; 191; Rozema *et al.* 1991c). It is unknown whether CO_2 enrichment will alleviate plant growth reduction caused by elevated UV-B. Another possible interaction between CO_2 and UV-B may be that plants with an increased growth rate under elevated carbon dioxide will be more susceptible to UV-B radiation than plants grown under ambient CO_2 (c.f. *Triticum aestivum* and *Elymus athericus* in Table 2). It is concluded that as plant species differ markedly in their response to increased UV-B and CO_2-enrichment, the outcome of combined CO_2 and UV-B treatment of plants is likely to be species-dependent, varying both qualitatively and quantitatively (Teramura *et al.* 1990).

CO_2 enrichment and water stress (drought and salinity)

Generally it has been indicated that reduced growth due to water stress can be counteracted by CO_2 enrichment (Strain & Cure 1985). The underlying mechanism of this CO_2 enrichment effect is reduced transpiration and increased water potential of the plant. Here literature will be discussed, reporting on studies of CO_2 enrichment and water stress.

CO_2 enrichment stimulates growth in many plant species. Physiologically, increased rates of net photosynthesis and reduced rates of transpiration may be involved. Rozema *et al.* (1991a) demonstrated increased growth in the C_3 salt marsh plants *Scirpus maritimus* and *Puccinellia maritima* with CO_2 enrichment in a greenhouse study. The relative increase in growth due to increased CO_2 was greater under high-salinity (250 mM NaCl) than under low salinity (10 mM NaCl). Similar results have been reported by Zeroni & Gale (1984). This implies that a salt induced growth depression may be partially alleviated by an atmospheric CO_2 increase. Schwarz & Gale (1984) reported increased growth in response to salinity for some C_3 and C_4 plant species, when grown at a (very) high level of carbon dioxide (2500 μmol mol^{-1}). A similar interaction between CO_2 enrichment and salinity stress was found for the C_4 glycophyte *Andropogon glomeratus* (Bowman & Strain 1987). This C_4 sedge occurs on the higher parts of North Carolina salt marshes. Leaf area and plant biomass decreased in control (0 mM NaCl) plants with increasing CO_2 (350, 500 and 650 μmol mol^{-1} CO_2). In salt-stressed plants (100 mM NaCl) leaf area and plant biomass was less, but increased with increasing carbon dioxide. Bowman & Strain (1987) reported reduced net photosynthesis and transpiration with increased salinity. There was decreased transpiration with CO_2 enrichment in salt-stressed plants, but not in control plants. There was no difference in net photosynthetic rate with increased carbon dioxide in plants grown in 0 mM NaCl and in 100 mM NaCl. Increased growth of salt-stressed plants with increasing CO_2 could therefore not be ascribed to increased carbon assimilation, but rather to improvements in leaf water relationships due to reduced transpirational water loss (Bowman & Strain 1987).

The effects of CO_2 enrichment and drought stress on growth of *Aster pilosus* (C_3) and *Andropogon virginicus* (C_4) have been analysed in relation to competition between these two old-field perennials (Marks & Strain 1989). It appeared that *Aster pilosus* was a stronger competitor than the broomsedge (*Andropogon*) under elevated CO_2. This indicates that improved growth of the C_3 species with elevated CO_2 and (partial) alleviation of drought stress with CO_2 enrichment has resulted in its increased competitive ability (cf. Bazzaz & Carlson 1984).

In a comparison of the response of the C_3 (*Aster pilosus*) and a C_4 (*Andropogon virginicus*) old field perennial to the joint action of CO_2 enrichment and drought stress, Wray & Strain (1986) found no significant interaction for the C_4 broom sedge. Drought-stressed *Aster* increased total plant biomass with CO_2 enrichment. For the C_3 plant *Aster*, predawn leaf water potentials were less negative for plants grown in increased CO_2, while for the C_4-plant *Andropogon* no such effect was found. The response of the C_3-plant can again be explained by a reduction of stomatal conductance at elevated CO_2. Thus, stomatal closure with carbon dioxide enrichment may enable *Aster* to avoid drought stress. Alleviation or partial alleviation of drought stress with elevated atmospheric carbon dioxide has also been reported by Sionit *et al.* (1981) and Morison & Gifford (1983). Wray & Strain (1986) confirmed that the C_3-species showed a stronger physiological response to elevated CO_2 than the C_4 species. Halophytic C_3-species of European salt marshes *Aster tripolium* and *Spergularia maritima* showed an increase in the mean relative growth rate with CO_2 enrichment (Rozema *et al.* 1990a), while salinity decreased the mean relative growth rate. Photosynthesis increased with elevated carbon dioxide and decreased with increased salinity cf. Rozema & van Diggelen (1991). The rate of transpiration decreased with elevated CO_2 and with raised salinity. The water potential of the shoot, measured with a Scholander's pressure bomb became more negative with increased salinity, and less negative with elevated CO_2. The C_3 salt marsh monocotyledonous species *Scirpus maritimus* and *Puccinellia maritima* showed an increase in RGR to increased carbon dioxide and salinity (Rozema *et al.* 1991a). The C_4-grass *Spartina anglica* did not show an increased relative growth rate with carbon dioxide enrichment. Water use efficiency of C_3 and C_4 species increased with elevated atmospheric CO_2. For *Scirpus maritimus* this increase could be related to an increased rate of net photosynthesis. For *Spartina anglica* (C_4) photosynthesis did not increase, but the rate of transpiration was significantly reduced. Shoot water potentials were less negative with CO_2 enrichment, especially at increased salinity. The relative increase in growth with elevated CO_2 was markedly higher at increased salinity. For these two C_3-salt marsh grasses CO_2 enrichment partially alleviated salinity stress (Rozema *et al.* 1991). A survey of the percentage biomass or growth increase with elevated atmospheric CO_2 at low and high salinity is presented in Table 3. Literature on the interactive effects of CO_2 enrichment and salinity has been reviewed earlier by Kimball (1985).

Further experiments (Lenssen & Rozema 1990; Lenssen *et al.* 1992, this volume, Rozema *et al.* 1991) have extended studies on the effects of CO_2 enrichment and salinity on salt marsh plants. The results confirm that CO_2 enrichment under greenhouse conditions (200 μmol m^{-2} s^{-1} (PAR), 24 °C day/18 °C night, 70% RH) improved the growth of the C_3-salt marsh grass *Elymus athericus*) (= *E. pycnanthus*) but not of the C_4 salt marsh grass *Spartina anglica*. It appeared that growth reduction induced by increased salinity, could be partially raised by carbon dioxide enrichment in the C_3-plant, but not in the C_4-species. In most cases net photosynthesis increased with CO_2 enrichment, and the rate of transpiration was reduced with elevated CO_2, while the shoot water potential became less negative with increase CO_2.

Improved growth of C_3 salt marsh species has also been demonstrated in field studies using open top chambers. In a long term study of CO_2 enrichment in a salt marsh dominated by *Scirpus olneyi* (C_3) and *Spartina patens* (C_4). Drake and co-workers (Curtis *et al.* 1989a and b; Arp 1992, this volume; Leadley & Drake 1992, this volume) have gathered unique results of CO_2 enrichment on salt marsh ecosystem characteristics. Biomass of *Scirpus olneyi* (C_3) increased by 20% with elevated CO_2, but there was no significant biomass increase for *Spartina patens* (C_4). Total daytime carbon dioxide assimilation was much higher with carbon dioxide enrichment in the *Scirpus* (C_3) vegetation than in *Spartina* (C_4) stands, while transpiration was reduced by 25–30% in both the C_3 and C_4 community of the salt marsh. These results provide evidence for the hypothesis that CO_2 enrichment stimulates plant growth via increased net photosynthesis and not via improved water relations. In the C_4 salt marsh species *Spartina patens*, the plant water potential (Ψ_T) was improved at elevated carbon dioxide but there was no effect on biomass increment. These data imply that increased photosynthesis at elevated CO_2 resulted in an increase in the biomass in the C_3 community (Curtis *et al.* 1989a; Curtis *et al.* 1989b; Rozema *et al.* 1991a).

In a greenhouse experiment (see Lenssen *et al.* 1992, this volume for experimental details) wheat and maize were grown at two levels of atmospheric carbon dioxide (350 and 750 μmol-mol^{-1}) and at two levels of salinity (0 and 100 mM NaCl) (Tables 2 and 3).

The Relative Growth Rate (RGR) of wheat and maize was reduced with increased salinity. The reduction of the growth rate with increased salinity was stronger in maize than in wheat, demonstrating that wheat is relatively more salt tolerant than maize. The Relative Growth Rate of wheat (C_3) was increased with carbon dioxide enrichment, while no such positive effect was found for maize (C_4) (Table 4). Remarkably, maize plants grown at elevated CO_2 (second harvest) suffered less from salt stress, than plants

Table 3. Increase (percentage of control) of growth of C_3 and C_4 plant species at elevated atmospheric CO_2 compared at low and high levels of salinity for C_3 and C_4 species cultivated in the greenhouse.

Plant species	Salinity treatment mM NaCl control-enhanced	CO_2 treatment μmol mol^{-1} ambient/elevated	Increase of growth at elevated CO_2 (%)		Comments	Reference
			Low salinity	High salinity		
Urtica dioica (C3)	0–25	350–700	5	31	Salt stress alleviation by CO_2 explained as a result of decreased stomatal conductance	Janssen *et al.* (1986)
Andropogon glomeratus (C4)	0–100	350–500–600	– 37	3		Bowman & Strain (1987)
Spergularia maritima (C3)	10–250	340–580	15	22	Less negative shoot water potential at elevated CO_2	Rozema *et al.* (1990)
Aster tripolium (C3)	10–250	340–580	22	– 5		
Elymus pycnanthus (C3)	0–100	400–750	34	34	Less negative shoot water potential at elevated CO_2, increased photosynthesis, reduced transpiration rate	Lenssen & Rozema (1990)
Aster tripolium (C3)	0–100	400–750	12	25		
Spartina anglica (C4)	0–100	400–750	– 10	8		
Scirpus maritimus (C3)	10–250	340–580	34	41	CO_2 enrichment related to increased leaf elongation in high salt Scirpus	Rozema *et al.* (1991)
Puccinellia maritima (C3)	10–250	340–580	71	95		
Elymus athericus (C3)	0–250	380–720	76	300 first harvest	Leaf area increased at elevated CO_2, SLA and LAR decreased	Lenssen *et al.* (1992)
(=*pycanthus*)	0–250	380–720	8	37 second harvest		
Triticum aestivum (C3)	0–100	350–750	6	– 21 first harvest	Leaf area increased for C3, not for C4 at elevated CO_2; reduced SLA and LAR for C3 and C4; photosynthetic acclimation involved in C3	Rozema (1992)
Zea mays (C4)	0–100	350–750	58	4 second harvest		
	0–100	350–750	– 6	– 49 first harvest		
	0–100	350–750	– 2	240 second harvest		

Table 4. Effect of atmospheric carbon dioxide enrichment and increased salinity in hydroponic culture on plant biomass (g), leaf area (cm^2) and root/shoot ratio of wheat (*Triticum aestivum*) and maize (*Zea mays*). Average values of six replicates with standard error of the mean. Data refer to two sequential harvests (I, II) with intervals of two weeks.

	CO_2 μmol mol^{-1}	NaCl mM	DW shoot	DW root	DW plant	Leaf area cm^2	Shoot:Root ratio
				Wheat (*Triticum aestivum*)			
I	350	0	0.22 ± 0.03	0.062 ± 0.005	0.286 ± 0.034	47.0 ± 5.6	3.62 ± 0.42
	350	100	0.15 ± 0.05	0.037 ± 0.009	0.186 ± 0.036	26.7 ± 4.9	6.95 ± 4.55
	750	0	0.24 ± 0.02	0.060 ± 0.005	0.304 ± 0.030	50.3 ± 3.4	4.07 ± 0.24
	750	100	0.11 ± 0.01	0.033 ± 0.003	0.147 ± 0.012	17.5 ± 1.23	3.55 ± 0.53
II	350	0	0.92 ± 0.10	0.157 ± 0.017	1.082 ± 0.117	212.7 ± 17.4	5.99 ± 0.56
	350	100	0.52 ± 0.03	0.087 ± 0.012	0.595 ± 0.082	82.3 ± 12.6	5.91 ± 0.31
	750	0	1.39 ± 0.13	0.327 ± 0.086	1.713 ± 0.147	269.1 ± 22.1	4.41 ± 0.40
	750	100	0.52 ± 0.03	0.091 ± 0.006	0.614 ± 0.042	61.4 ± 3.5	5.82 ± 0.45
				Maize (*Zea mays*)			
I	350	0	0.28 ± 0.13	0.217 ± 0.009	0.50 ± 0.04	76.5 ± 7.4	1.28 ± 0.11
	350	100	0.20 ± 0.06	0.205 ± 0.015	0.41 ± 0.03	46.0 ± 5.4	0.98 ± 0.16
	750	0	0.26 ± 0.02	0.210 ± 0.009	0.47 ± 0.05	82.5 ± 10.3	1.22 ± 0.18
	750	100	0.20 ± 0.02	0.194 ± 0.019	0.39 ± 0.05	55.2 ± 9.4	1.00 ± 0.09
II	350	0	1.45 ± 0.04	0.453 ± 0.060	1.90 ± 0.17	414.5 ± 39.2	3.22 ± 0.40
	350	100	0.22 ± 0.03	0.122 ± 0.026	0.35 ± 0.08	31.9 ± 25.8	1.80 ± 0.28
	750	0	1.28 ± 0.03	0.374 ± 0.078	1.65 ± 0.33	317.0 ± 82.4	3.42 ± 0.38
	750	100	0.64 ± 0.03	0.198 ± 0.012	0.84 ± 0.12	122.6 ± 25.6	3.18 ± 0.48

grown at ambient atmospheric CO_2. Since NAR is not stimulated by CO_2 enrichment, this may be due to reduced transpiration and improved water relationships (Table 6). However the relative growth rate of the maize plants, grown in a greenhouse with about 200 μmol m^{-2} s^{-1} PAR, is much lower than under increased light intensity in the greenhouse or when grown in the field with full sun light. Therefore the results for maize should be interpreted with care. The positive growth response of wheat to CO_2 enrichment is related to an increased net assimilation rate, while the Leaf Area Ratio and the specific leaf area are unaltered or decreased with increased carbon dioxide (Table 5). The Leaf Weight Ratio did not change with increased carbon dioxide in wheat. For maize the Net Assimilation Rate (NAR) did not increase with increased carbon dioxide, and Leaf Area Ratio (LAR) and Specific Leaf Area (SLA) increased with carbon dioxide enrichment (first harvest), the Leaf Weight Ratio was unaffected at elevated CO_2 (first harvest). Similarly, den Hertog & Stulen (1990), studying *Plantago major* and *Urtica dioica*, found that the Leaf Weight Ratio (LWR) and root/shoot ratio was not affected by CO_2 enrichment. Net photosynthesis of wheat increased with increased carbon dioxide but not in maize, while the transpiration rate decreased with high carbon dioxide in both species (Table 6). The growth rate depression with increased salinity is not alleviated by carbon dioxide enrichment. This may relate to the result that LAR and SLA of wheat are depressed by increased CO_2. Under non-saline conditions the leaf area of the shoot of wheat increased with carbon dioxide enrichment but not the LAR and SLA. This may be explained by an increase in the starch content of wheat leaves with increased carbon dioxide, which was not found in maize (Table 7). With increased salinity the starch content

Table 5. Relative growth rate and growth parameters NAR, LAR, LWR and SLA of wheat (*Triticum aestivum*) and maize (*Zea mays*) cultivated in nutrient solution with increased salinity and with atmospheric carbon dioxide enrichment. Average values of six replicates and standard error of the mean. The data refer to two sequential harvests (I and II) with intervals of two weeks.

	CO_2 $\mu l\,l^{-1}$	NaCl mM	RGR $g\,g^{-1}\,day^{-1}$	NAR $g\,m^{-2}\,day^{-1}$	LAR $m^{-2}\,kg^{-1}$	LWR $g\,g^{-1}$	SLA $m^2\,kg^{-1}$
				Wheat (*Triticum aestivum*)			
I	350	0	0.135 ± 0.009	9.37 ± 0.63	16.2 ± 0.80	0.802 ± 0.019	21.0 ± 0.9
	350	100	0.101 ± 0.017	7.73 ± 1.36	14.1 ± 0.41	0.775 ± 0.025	18.1 ± 1.2
	750	0	0.141 ± 0.005	9.70 ± 0.50	17.0 ± 0.72	0.801 ± 0.024	22.5 ± 0.8
	750	100	0.093 ± 0.009	8.07 ± 0.77	12.4 ± 0.38	0.771 ± 0.043	16.3 ± 1.3
II	350	0	0.089 ± 0.005	4.87 ± 0.32	20.5 ± 0.73	0.852 ± 0.009	23.0 ± 0.8
	350	100	0.090 ± 0.009	6.68 ± 1.04	14.7 ± 0.44	0.854 ± 0.006	16.2 ± 0.6
	750	0	0.115 ± 0.006	7.18 ± 0.39	16.0 ± 0.40	0.807 ± 0.019	20.0 ± 1.2
	750	100	0.099 ± 0.007	9.36 ± 0.55	10.1 ± 0.36	0.851 ± 0.009	12.1 ± 0.4
				Maize (*Zea mays*)			
I	350	0	0.037 ± 0.005	3.67 ± 0.52	15.2 ± 1.05	0.556 ± 0.020	28.4 ± 2.7
	350	100	0.023 ± 0.005	2.78 ± 0.64	11.2 ± 0.48	0.474 ± 0.040	23.9 ± 2.0
	750	0	0.032 ± 0.006	2.94 ± 0.63	18.2 ± 1.49	0.532 ± 0.040	34.1 ± 5.2
	750	100	0.019 ± 0.008	1.94 ± 0.83	14.1 ± 0.78	0.496 ± 0.022	26.8 ± 1.7
II	350	0	0.092 ± 0.006	4.92 ± 0.49	21.9 ± 1.5	0.765 ± 0.019	29.3 ± 1.6
	350	100	- 0.017 ± 0.011	- 2.22 ± 1.30	8.8 ± 1.2	0.640 ± 0.040	12.2 ± 2.4
	750	0	0.056 ± 0.015	3.07 ± 0.69	31.4 ± 11.9	1.314 ± 0.542	24.2 ± 1.9
	750	100	0.049 ± 0.007	3.63 ± 0.45	14.0 ± 1.6	0.742 ± 0.034	17.8 ± 1.5

Table 6. Rate of net photosynthesis (Pn) (μmol CO_2 $m^{-2}\,s^{-1}$) and rate of transpiration (E) (mmol H_2O $m^{-2}\,s^{-1}$) of leaves of wheat and maize grown in hydroculture at two levels of atmospheric carbon dioxide and two levels of salinity. Average values of four replicates with standard error of the mean.

CO_2	NaCl	Wheat		Maize	
μmol mol^{-1}	mM	Pn	E	Pn	E
350	0	9.5 ± 0.6	5.17 ± 0.67	5.7 ± 0.4	1.50 ± 0.15
350	100	8.3 ± 1.2	3.81 ± 0.41	7.2 ± 1.5	1.83 ± 0.38
750	0	11.0 ± 1.55	3.21 ± 0.33	8.1 ± 0.9	1.44 ± 0.09
750	100	10.6 ± 0.73	4.84 ± 0.43	5.0 ± 0.5	0.94 ± 0.15

of the wheat leaves decreased. In maize the leaf area increased with CO_2 enrichment, LAR and SLA also increased, in particular during the interval of the first harvest.

In conclusion, the results for wheat show that the growth reduction caused by increased salinity is not alleviated or only partially alleviated by increased atmospheric carbon dioxide. Under non-saline conditions growth of wheat increased with elevated carbon dioxide due to increased NAR (cf. Jansen *et al.* 1986), and there was a raised rate of net photosynthesis while the transpiration rate was reduced. With increased salinity NAR was still higher at elevated CO_2 but LAR and SLA were depressed. This is caused by a reduction in the leaf area of the wheat shoot with increased salinity, probably as a result of reduced cell expansion. With carbon dioxide enrichment

Table 7. Content of starch (mg·g^{-1}·FW) of leaves of wheat (*Triticum aestivum* cv Obelisk) and of maize (*Zea mays* cv Limagrain 5) grown in hydroculture at two levels of carbon dioxide in the atmosphere (μmol mol^{-1} CO_2) and two levels of salinity. Average value of four replicates with standard deviation.

CO_2 μmol mol^{-1}	NaCl mM	Wheat	Maize
350	0	5.17 ± 1.61	9.10 ± 0.29
350	100	0.21 ± 0.04	19.78 ± 13.91
750	0	10.22 ± 0.45	12.90 ± 4.78
750	100	1.08 ± 0.21	12.20 ± 0.47

stomata of wheat leaves partially closed and the shoot water potential was increased (Table 1; Lenssen & Rozema 1990; Rozema *et al.* 1991a). However, no increase of LAR and SLA occurred with CO_2 enrichment combined with increased salinity. This could be expected when increased turgor potential would lead to raised cell and leaf tissue expansion and thus to increased leaf area.

The often postulated interaction between CO_2 enrichment and salinity, implying that salt stress may be (partially) alleviated by increased CO_2, did not occur in this experiment. In maize the leaf area was increased with elevated carbon dioxide combined with increased salinity as were LAR and SLA. The two glycophytic cereal crops wheat and maize appear to differ in their response to carbon dioxide enrichment in combination with increased salinity. Wheat and maize were chosen for this CO_2 x salinity greenhouse experiment because of rapid growth and homogeneous seedling

Table 8. Survey of effects of CO_2 enrichment, salinity and enhanced UV-B radiation of plants, based on single treatment (stress factor) studies discussed in this paper. + positive effect, – negative effect, o no effect, ? effect unknown. References in brackets.

	CO_2 enrichment		Salinity		Enhanced UV-B-radiation	
Relative Growth Rate	+	(1, 2, 5, 6, 7)	–	(14, 16, 25)	–	(9, 20, 23, 24)
Leaf Area Ratio	o/–	(1, 2, 5, 6, 11)	–	(14, 16, 25)	o	(21)
Leaf Area	+	(1, 10, 11)	–	(16, 25)	?	
Leaf Weight Ratio	o	(5, 6, 10, 11)	o	(18, 25)	o	(20)
Specific Leaf Area	o/–	(1, 2, 5, 6, 1)	–	(14, 16)	o	(21)
Net Assimilation Rate	+	(1, 2, 7)	o/+	(16, 25)	–	(21, 23, 24)
Net Photosynthesis	+	(1, 2, 7)	o/	(16, 25)	–	(20, 21, 23, 24)
Dark respiration	–	(1, 2, 7, 12)	+	(1, 25)	?	
Starch accumulation	+	(12, 26)	–	(25)	?	
Transpiration	–	(3, 10, 13, 15, 19)	–	(14, 18, 25)	–/o/+	(20, 23)
Shoot water potential	+	(3, 10, 11, 19)	–	(17, 25)	?	
Water use efficiency	+	(3, 10, 11, 19)	+	(17, 25)	+/–	(16, 21)

References

1. Allen (1990)
2. Bazzaz (1990)
3. Bowman & Strain (1987)
4. Delucia *et al.* (1985)
5. den Hertog & Stulen (1990)
6. den Hertog *et al.* (1992)
7. Houghton *et al.* (1990)
8. Kimball (1985)
9. Krupa & Kickert (1989)
10. Lenssen & Rozema *et al.* (1990)
11. Lenssen *et al.* (1992)
12. Poorter *et al.* (1988)
13. Strain & Cure (1985)
14. Rozema (1991)
15. Rozema *et al.* (1990a)
16. Rozema *et al.* (1990b)
17. Rozema *et al.* (1991a)
18. Rozema *et al.* (1991b)
19. Rozema *et al.* (1991c)
20. Staay *et al.* (1990)
21. Staay *et al.* (1992)
22. Stulen & den Hertog (1992)
23. Teramura (1987)
24. Teramura *et al.* (1990)
25. Van Diggelen (1988)
26. Wong (1990)
27. Warrick *et al.* (1986)

size and morphology in comparison with plant species from natural coastal ecosystems. Maize appeared to be more salt-sensitive than wheat. Such a difference in salt-sensitivity occurring at the chosen level of increased salinity (100 mM NaCl) may influence the plant response to combined elevated CO_2 and salinity.

Leaf area and stomatal index in response to elevated atmospheric CO_2

Leaf area per wheat plant may increase 26% with atmospheric carbon dioxide increasing from 350 to 750 μlmol mol $^{-1}$ while no such increase was found in maize (Table 4). LAR (m^2 leaf area per kg plant biomass) tends to decrease with increased atmospheric carbon dioxide in wheat plants. SLA (m^2 leaf area per kg leaf biomass) tended to decrease as well with elevated atmospheric carbon dioxide and appeared to be the cause of the reduction of LAR, since the Leaf Weight Ratio was unaffected (Table 5).

The increase of the leaf area per plant with increased atmospheric carbon dioxide may be related to the decline of stomatal density as reported by Woodward (1987) and Woodward (this volume). However, details on the effects of carbon dioxide enrichment on the morphology and architecture of the individual leaf are uncertain. Some reports (Lenssen *et al.* 1992, this volume, den Hertog *et al.* 1992, this volume; Tables 3 and 4, this paper) indicate a decrease of SLA with elevated CO_2. This does not imply that individual leaves will have a smaller leaf area. In fact Lenssen *et al.* (1992, this volume) report not only increased leaf area per plant but also increased area of individual leaves with atmospheric carbon dioxide enrichment. The decrease in SLA with elevated CO_2 (Table 5) may be the result of an increased leaf area and a relatively stronger increase of the leaf biomass, due to starch accumulation (Table 5). Stomatal densities of leaves of *Aster tripolium* did not decrease with CO_2 enrichment, but increased markedly with increased salinity (Rozema *et al.* 1991c). This finding indicates that environmental factors other than atmospheric carbon dioxide alone, affect stomatal density. Woodward's (1987) results are based on a comparison of contemporary plants with herbarium plant material of the pre-industrial (1800–1900) period. If the reported decrease of stomatal density with atmospheric CO_2 increasing from 280 μmol mol^{-1} (pre industrial level) to 340 μmol mol^{-1} CO_2 (1987) would be confirmed, it implies that the global increase of atmospheric carbon dioxide has already affected the biosphere.

CO_2 enrichment and flooding, recycling of CO_2 in partially submerged angiosperms

Salt marshes are flooded with sea water. Salinity and the direct and indirect consequences of inundation govern the physiology and ecology of salt marsh plants (Rozema *et al.* 1988). As flooding may affect transpiration and photosynthesis, interactive effects of elevated CO_2 and flooding may be expected. However, inundation did not affect the response to CO_2 enrichment in *Spartina anglica* (Lenssen *et al.* 1992, this volume).

In hydroponic culture Rozema *et al.* (1990a and 1991a) studied the effect of CO_2 enrichment in combination with aerated or hypoxic root conditions. Plant growth was reduced with hypoxic conditions but no significant interactions were found with CO_2 enrichment in the (C_3-) salt marsh species *Spergularia maritima*, *Aster tripolium*, *Scirpus maritimus* and *Puccinellia maritima*. To my knowledge there is no other literature on the interactive effect of flooding and atmospheric carbon dioxide enrichment on plants.

Under acid conditions, CO_2 concentrations are low in fresh water in equilibrium with the atmosphere. Some isoetid, phanerogams and other aquatic plants are adapted to low CO_2 concentrations. The submersed cyperid aquatic species *Juncus bulbosus* is common in acid lakes (Wetzel *et al.* 1984). *Juncus bulbosus* uses CO_2 from respiratory sources recycled internally and transported within the gas lacunal system. The lacunae in the tissue of *Juncus bulbosus* allow connections to the various sites of CO_2 production within the plant, such as dark respiration and photorespiration and outside the plant roots, respiration of rhizosphere microorganisms (Wetzel *et al.* 1984). Brix (1988) reports a concentration of 5000 μmol-mol^{-1} CO_2 in the air-filled space in the shoot and even higher concentrations in the aerenchyma of the roots of the halophyte *Phragmites australis*. More generally, the CO_2 concentration in lacunae and air tissue of roots, stems and leaves is in the range of 1000 μmol mol^{-1}.

Root porosity generally increases with the lowering of redox potential under anaerobic and water-logged conditions. It is therefore expected that the importance of an internal CO_2-recycling route in comparison with the uptake of CO_2 from the atmosphere will increase with more pronounced flooding conditions. Absorption of carbon dioxide by roots may, in principle, occur in vascular land plants (Bergquist 1964; Yoshida *et al.* 1974). In experimental studies of the salt marsh plants *Puccinellia maritima*, *Elymus pycnanthus* and *Scirpus maritima* which have a well developed aerenchyma system, there was increased growth under elevated CO_2, but no significant interaction for the CO_2 enrichment with flooding conditions (Rozema *et al.* 1991a; Lenssen *et al.* 1992, this volume). This report therefore does not support the hypothesis of recycling of CO_2 from the root and from microbial respiration in (salt) marsh plant species. The difference between the (completely) submerged *Juncus bulbosus* and the salt marsh plant *Puccinellia maritima* (with only the root and lower part of the shoot temporarily submerged) is, that a major part of the shoot of the latter species is capable of rapid gas exchange of CO_2 from the atmosphere.

In fact, there is a gradual transition from completely emergent higher plants to completely submerged higher plants. It is expected that partially submerged plants with recycling of CO_2 will respond less to atmospheric CO_2 enrichment than completely emerged angiosperms. To our knowledge, however, there are no published reports on the possibility of the recycling of CO_2 in partially submerged coastal and inland marsh plants.

Terrestrial plants with atmospheric carbon dioxide as the sole carbon source for carboxylation respond generally to CO_2 enrichment. Completely submerged angiosperms and other plants in marine and freshwater aquatic ecosystems will not respond to increasing levels of atmospheric carbon dioxide. As yet, there is no evidence that partially submerged marsh plants and salt marsh plants recycle internal CO_2 as fully submerged angiosperms do. Of all vascular terrestrial plants only *Stylites andicola*, lacking stomata, absorbs CO_2 for photosynthesis via its roots (Keeley *et al.* 1984). Field experiments with open top chambers would allow a comparison of the responsiveness of marsh plants and non-helophytes to elevated CO_2. In addition to the greenhouse and field experiments with inundation treatments and atmospheric carbon dioxide enrichment, ^{14}C labelling and $^{13}C/^{12}C$ experiments (cf. Guy & Reid 1986) will be helpful to identify a possible CO_2 supply route from the rhizosphere to the carboxylation sites in the leaves.

Plant responses to carbon dioxide enrichment and interactions with soil and atmospheric conditions: integration by analysis of growth parameters

Relative growth rate is generally reduced with increased salinity primarily as a result of reduced SLA. Accumulation of sodium and chloride in the leaf tissue may cause reduced net photosynthesis, but it does not usually occur in an early phase of growth and it is less important than the salinity-induced reduction of LAR and SLA (this paper; Rozema *et al.* 1991b). CO_2 enrichment could alleviate salt and drought stress as a result of reduced transpiration and increased net CO_2 assimilation. Decreased stomatal conductance and increased shoot water potentials have indeed been reported (Bowman & Strain 1987; Marks & Strain 1987; Curtis *et al.* 1989; Marcelis 1989; Marks & Strain 1989; Rozema *et al.* 1990; Rozema *et al.* 1991). If an increased shoot water potential relates to increased turgor or to changes in the hormone balance, CO_2 enrichment could lead to increased cell expansion (Sasek & Strain 1989; Rozema *et al.* 1991a) and increased SLA and LAR either through turgor regulation (Sionit & Patterson 1985) or through cell wall loosening processes. However, CO_2 enrichment does not significantly affect or reduce LAR and SLA (Table 3; Allen 1990; Bazzaz 1990). This may be the result of accumulation of starch when sinks for photosynthates are not available or when the capacity to load assimilates into the phloem is too low. Also, leaves may grow thicker, rather than developing more leaf area. When thicker leaves contain more layers of palissade parenchyma increased photosynthetic utilization of photons would lead to an increased NAR. No measurements of leaf thickness under conditions of CO_2 enrichment are known. Lenssen *et al.* (1992, this volume) reported a relatively high growth response to elevated CO_2 at increased salinity. It is hypothesized that increased respiration at high salinity represents a sink for photosynthates, thus delaying or deleting acclimation to elevated CO_2 (Poorter *et al.* 1988). It is not known, how important the decline of the growth response of a plant with time is to enhanced CO_2, does it only occur in short-term greenhouse or climate room studies, does it occur under field conditions in long-term studies? Arp & Drake (1991) report an increased photosynthetic capacity in a C_3 salt marsh species after four years of exposure to elevated CO_2, suggesting that acclimation to elevated CO_2 does not occur in field studies. In reviewing the effects of a joint increase of atmospheric CO_2 and elevated UV-B radiation on plants no significant interactive effect has as yet been found (Rozema *et al.* 1990; van de Staaij *et al.* 1992, this volume), Teramura *et al.* 1990 indicate a modification of the CO_2-induced biomass increase by elevated UV-B radiation. As with the $CO_2 \times$ salinity interaction, studies on the $CO_2 \times$ UV-B interaction need great care with methodology and the interpretation of the results (cf. Table 2). As CO_2 enrichment and enhanced UV-B radiation affect different parts of the photosynthetic apparatus (carboxylation and photosystem II processes, respectively) additive effects of CO_2 and UV-B in combined treatments may theoretically be expected. However, UV-B induced disfunctioning of stomata and UV-B affected photosynthesis, or a CO_2 induced growth increase may lead to non-additive CO_2 and UV-B interaction effects. Global climatic change involves the simultaneous increase of atmospheric CO_2, UV-B and temperature. Therefore modelling and experimental assessment of the impact of CO_2 enrichment and interactions with related environmental factors is a major research requirement of the near future.

Conclusions and recommendations

In this review paper it has been attempted to analyse interactive effects of CO_2 enrichment and soil and atmospheric environmental conditions. Of the possible interactions, the $CO_2 \times$ UV-B interactions has only scarcely been examined experimentally. The sparce results indicate that the response of plants to CO_2 enrichment can be modified by enhanced UV-B, although no statistically significant interactions have been reported.

Remarkably few studies are available on the interactive effects of CO_2 enrichment and salinity. There is some evidence that atmospheric carbon dioxide enrichment partially alleviates salinity induced growth reduction. CO_2 enrichment probably helps to improve water relations by (partial) stomatal closure and less negative plant water potentials. Most $CO_2 \times$ salinity studies have been performed in pot, hydroculture or soil culture in the greenhouse. Evidence is growing for acclimation of the photosynthetic response to CO_2 enrichment relating to small pot size (Idso & Kimball 1991; Arp 1991). Salinity causes increased dark respiration, and increased sink strength for photosynthates. As a result photosynthetic acclimation will be delayed. Thus, a $CO_2 \times$ salinity interaction may also consist of a CO_2 interaction with a methodological artifact i.e. acclimation depending on pot size, and availability of nutrients and resources. For both $CO_2 \times$ salinity and $CO_2 \times$ UV-B interactions field studies as combined with Open Top Chamber or Free Air CO_2 Enrichment studies will avoid some of the methodological difficulties associated with pot culture and greenhouse studies (acclimation, relatively low photosynthetic photon fluence).

For all environmental factors that can interact with CO_2 enrichment, plant responses will be species-specific, because of differential sensitivity to increased salinity, enhanced UV-B radiation, water stress, nutrient deficiency etc. Assessment of the response of the biosphere to global change including the climate change (e.g. CO_2 enrichment and enhanced solar UV-B radiation) requires careful methodology and detailed analysis of effects of combinations of relevant environmental conditions (e.g. $CO_2 \times$ temperature, $CO_2 \times$ UV-B).

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