A Field Study of the Effects of Elevated CO_2 on Ecosystem Processes in a Chesapeake Bay Wetland

Bert G. Drake

Smithsonian Environmental Research Center, PO Box 28, Edgewater, MD 21037, USA.

Abstract

Open top chambers are being used in a long-term project to determine the effects of elevated CO_2 on ecosystem processes on a Chesapeake Bay wetland. Three communities are studied: mono-specific stands of the C_3 sedge, *Scirpus olneyi*, and the C_4 grass, *Spartina patens*, and a mixed community of these two species and the C_4 grass, *Distichlis spicata*. Treatment began in the spring of 1987 and will continue through the 1994 growing season.

During the first 4 years of exposure, elevated CO_2 had the following effects on mono-specific stands of the C_3 sedge, *Scirpus olneyi*: increased quantum yield and photosynthetic capacity, reduced dark respiration, increased numbers of shoots, roots and rhizomes, reduced nitrogen concentration of all tissues, increased nitrogen fixation and increased ecosystem carbon accumulation. In a mixed community of the sedge and C_4 grass species, *Spartina patens* and *Distichlis spicata*, biomass of the C_3 component increased over 100% and this was accompanied by decreased biomass in the C_4 component of the community. Elevated CO_2 reduced water loss, increased water potential and delayed senescence in all three species.

Many factors contributed to CO_2 stimulated carbon accumulation in the plant community dominated by the C_3 sedge, *Scirpus olneyi*, including: sustained high photosynthetic capacity, decreased respiration, delayed senescence, and allocation of the additional carbon to roots and rhizomes. The complex interaction of these diverse responses suggests that the rising atmospheric CO_2 may have a significant impact on ecosystem processes.

Introduction

Rising atmospheric CO_2 concentration is projected to reach twice the pre-industrial value of about 280 ppm by the middle of the 21st century and result in significant changes in global climate (Houghton and Woodwell 1989). But there is considerable uncertainty regarding the future rate of CO_2 increase, the geographic distribution and magnitude of the projected warming, and especially the consequences of warming for other climate factors such as atmospheric and soil moisture (Houghton *et al.* 1990; (R. S. Lindzen, personal communication; Singer *et al.* 1991). On the other hand, there is considerable evidence that elevated CO_2 concentration increases plant growth. The growth stimulation caused by elevated CO_2 is primarily a consequence of a fundamental property of photosynthetic CO_2 assimilation in all green plants, namely increased photosynthetic carbon assimilation resulting from the competitive inhibition of the oxidase activity of Rubisco* by CO_2 (Lorimer 1981). Because the

*Abbreviations used: Rubisco, D-ribulose-1,5-bisphosphate carboxylase–oxygenase; C_a, partial pressure of CO_2 in the air surrounding the leaf (kPa); A, rate of CO_2 assimilation per unit of projected stem area (μmol m^{-2} s^{-1}); A_{sat}, A at light saturation (μmol m^{-2} s^{-1}); NCE_a, net CO_2 exchange per unit ground area within the closed top chamber (μmol m^{-2}s^{-1}); ET, evapotranspiration per unit ground area (mmol m^{-2} s^{-1}); NCE_b, NCE per unit green biomass within the closed top chamber (μmol g^{-1} s^{-1}); Q, photosynthetically active photon flux (μmol m^{-2} s^{-1}); Q_{abs}, Q absorbed per unit of projected stem area; ϕ_{abs}, maximum quantum yield (dimensionless); LCP, light compensation point of photosynthesis (μmol m^{-2}s^{-1}); PPF, photosynthetic photon flux in the 400-700 nm bandwidth of sunlight; R, dark respiration per unit dry weight of stem (μmol g^{-1} s^{-1}).

oxidase activity of Rubisco increases more rapidly with temperature than carboxylation (Jordan and Ogren 1984), stimulation of photosynthesis by rising atmospheric CO_2 is expected to be significantly greater in warm than in cooler climates and intensified by global warming (Long 1991; Long and Drake 1992). The stimulation of growth by elevated CO_2 is also altered by environmental factors that modify the sink capacity (Stitt 1986, 1991). Nevertheless, a very large data set consisting of over 400 experiments provides overwhelming evidence that elevated CO_2 stimulates plant growth (Kimball 1983; Cure and Acock 1986).

The importance of the vegetation response to rising CO_2 for global climate change is that terrestrial ecosystems may be a substantial sink. But, as with most other aspects of this problem, there are advocates for the opposite view, namely that rising temperature will increase microbial respiration and the terrestrial source of CO_2 will result in a runaway greenhouse effect (Woodwell 1978; Woodwell *et al.* 1978; Shaver *et al.* 1982; Houghton *et al.* 1985; Houghton and Woodwell 1989).

Most of the work on the CO_2 effects on plants has been carried out with greenhouse grown horticultural and crop species, although some experiments with wild species and juvenile trees have also been reported (Eamus and Jarvis 1989). Experiments with perennial grasses and trees are particularly important because these probably account for the largest amount of carbon exchange between the atmosphere and the biosphere. Very few studies have been conducted with perennial species in the field under the varying conditions of natural environments and, apart from the study reported here, only four studies have attempted continuous CO_2 treatment of perennial species over the course of several growing seasons (Grulke *et al.* 1990; Overdieck 1990; Idso *et al.* 1991; J. M. Ham, personal communication).

The study reviewed in this paper was designed to examine the responses of three mature plant communities in their native habitat to elevated atmospheric CO_2. The overall goal of the project is to determine how the expected stimulation of carbon assimilation would modify ecosystem processes. Three plant communities in a saltmarsh ecosystem were exposed to elevated CO_2 for four continuous seasons. Standing biomass, root production, dark respiration and photosynthesis in individual leaves were studied, and ecosystem gas exchange was periodically monitored.

Data emerging from this study offer a different perspective on the potential for terrestrial ecosystems to act as a sink for anthropogenic carbon than is obtained from laboratory experiments or the models based on them. While the effects of elevated CO_2 are clearly dominated by direct effects on photosynthesis, the overall conclusion from this study is that elevated CO_2 alters many processes important in the ecosystem carbon budget, with the result that total carbon accumulation was greater than anticipated.

Methods

The study site on the Kirkpatrick Marsh was chosen because vegetation in brackish marshes on the Chesapeake Bay is organised into mono-specific stands of C_3 and C_4 type species occurring side by side with mixtures of the same species. This feature of wetlands provides a unique opportunity to test the effects of elevated CO_2 on species having fundamentally different capacities to respond to a CO_2-rich atmosphere. In this sense, the C_4 community provided an internal control for the experimental approach. We used the following stands: a stand dominated by the C_3 sedge, *Scirpus olneyi*; a stand dominated by the C_4 grass, *Spartina patens*; and a stand in which these two species were present with the C_4 grass clearly in the dominant position occupying 70-90% of the biomass. These three stands are referred to as the *Scirpus, Spartina,* and mixed communities. A second C_4 grass, *Distichlis spicata*, also occurred in the mixed community but the biomass of this species was approximately 30-50% of the biomass of *Spartina patens*. Additional details of the species composition and distributions in the study sites are found in (Arp 1991*b*). A survey of the three communities showed that the species combinations were found within narrow elevational limits: the C_4 species, *Spartina patens* and *Distichlis spicata*, were almost always found at higher, more emergent and therefore more saline regions than the more frequently flooded C_3 species, *Scirpus olneyi*. Additional details of the site are available in other publications and reports, copies of which may be obtained from the author of this paper (Drake *et al.* 1987,1988; Curtis *et al.* 1989*a;* Arp 1991*b*).

Study plots were located in a blocked design with two plots having chambers and the third being a control plot. One of the two paired chambers received normal ambient air and the other received enough additional CO_2 to increase the concentration to twice the present normal ambient level. Chambers were taped to rings of plastic garden edging which had been inserted approximately 10 cm into the marsh soil to isolate the surface roots within the chamber and provide a gas-tight seal.

The concentration of CO_2 within the chambers was controlled by manual regulation of the flow of pure CO_2 through a manifold and individual flowmeters to reach a target of 340 ppm above normal ambient concentration which was maintained 24 h each day. The CO_2 treatment was begun in April when green shoots first appeared and ended in November, usually with the first snow storms of winter. Mean values of the two treatments for the growing season of 1988 were 343 ± 16 ppm for the plants exposed to normal ambient CO_2 and 681 ± 34 ppm for the enriched CO_2 treatment (Curtis et al. 1990). The marsh was often frozen between mid-December and mid-February and there was no treatment during this period.

Additional details of the chamber design and microclimate and the method for determining ecosystem gas exchange can be found in Drake et al. (1989) and Leadley and Drake (1992).

Results

Physiological Responses in Individual Plants and Tissues

(1) Photosynthesis: light and CO_2 responses

The data on effects of elevated CO_2 on the photosynthetic responses of the C_3 plant, *Scirpus olneyi* are summarised in Table 1. Elevated CO_2 had little effect on anatomy associated with photosynthesis but did have significant effects on nitrogen content and chlorophyll. The increase in leaf level photosynthesis was reflected in the canopy measurements.

Table 1. Summary of the responses of the photosynthetic apparatus of the C_3 sedge, *Scirpus olneyi*, to long-term exposure to normal ambient and elevated CO_2 concentration
The data are means and standard errors and the probability for significant differences between the means as determined by Student's *t*-test

	pCO_2 during growth (ppm)		n	$P<$
	343	681		
Anatomy				
Cross sectional area (mm^2)	4.0±1	4.5±1.4	10	0.39
Stomatal density (No. mm^{-2})	166±6.6	177±2.9	18	0.14
Specific leaf weight(gdw mm^{-2})	260±8.0	274±1.6	25	0.10
Tissue chemistry				
N concentration (mg gdw^{-1})	11.2±0.2	9.5±0.2	5	0.002
Total chlorophyll (mg gfw^{-1})	1.68±0.06	2.1±0.11	6	0.007
Chlorophyll *a/b*	1.93±0.05	1.55±0.04	6	0.001
Light responses				
Quantum yield (mmol CO_2 mol^{-1} PPF$_{abs}$)	65.0±3.0	78.0±3.0	10	0.003
LCP (μmol m^{-2} s^{-1})	51.0±3.0	31.0±3.0	10	0.001
CO_2 responses				
Carboxylation efficiency (μmol m^{-2} s^{-1})	66.6±7.9	94.9±9.3	6	0.06
CO_2 compensation point (ppm)	102±2.0	105±2.4	6	0.36
A at 350 ppm (μmol m^{-2} s^{-1})	6.6±0.5	8.7±0.23	6	0.006
A at 680 ppm (μmol m^{-2} s^{-1})	12.2±0.9	16.0±0.9	6	0.018
Canopy responses				
Net ecosystem CO_2 exchange (mol m^{-2} d^{-1})	0.84±0.1	0.41±0.2	5	0.01

(a) *Maximum light saturated photosynthesis*. Photosynthetic light response curves were determined in the field by Ziska *et al.* (1990) using an ADC portable infra-red gas analyser and a Parkinson leaf chamber fitted with neutral density filters made of stainless steel mesh. They showed that there was a very large response to elevated CO_2 in the C_3 sedge, *Scirpus olneyi*, averaging approximately 70% during midsummer when temperature was 30-35°C, but very little response to increased CO_2 in the C_4 grass, *Spartina patens*. There was essentially no difference between the responses to light in the plants grown in normal ambient CO_2 and those grown in elevated CO_2. An increase in temperature from 31 to 35°C increased the response of photosynthesis to elevated CO_2 about the same amount in plants grown in either normal ambient CO_2 or elevated CO_2 (Ziska *et al.* 1990).

(b) *Quantum yield and LCP*. An integrating sphere modified to include a gas exchange chamber (Ireland *et al.* 1989) was used to measure net CO_2 exchange (A) and absorbed PPF (Q_{abs} = 400-700 nm) at photon flux <200 μmol m^{-2} s^{-1}. These measurements were used to determine the light compensation point (LCP) and quantum yield ($\phi_{abs} = A/Q_{abs}$; μmol CO_2/μmol PPF)(Long and Drake 1991). The quantum yield increased approximately 20% from 0.065 in normal ambient CO_2 to 0.078 in elevated CO_2 at 28°C and LCP declined 40% from about 50 to 30 μmol m^{-2} s^{-1}. These responses were characteristic of all leaves whether grown in elevated or normal ambient CO_2. The light response data provide no evidence of acclimation in the efficiency of transduction into NADPH and ATP on the photosynthetic membrane. A model of canopy photosynthesis was parameterized using the measured values of quantum yield and LCP (Long and Drake 1991). The results of the model runs using environmental and plant parameters for 12 June 1988 (0.63 and 1.06 mol m^{-2} s^{-1} for the normal ambient and elevated CO_2 treatments respectively) were compared to measured values of canopy photosynthesis in the field on this date (0.61 and 1.07 mol m^{-2} s^{-1} for normal ambient and elevated CO_2 treatments). This exercise demonstrated that the increase in quantum yield and decline in LCP was responsible for a 16% increase in total daily photosynthesis.

(c) CO_2 *responses*. The response of photosynthesis to CO_2 was determined in the field on attached stems of the C_3 plant, *Scirpus olneyi*, using a temperature controlled open gas exchange system (Arp and Drake 1991). A/C_i curves constructed from measurements of water vapour conductance and net CO_2 exchange showed that after 4 years' exposure to elevated CO_2 this C_3 plant had an increased capacity to assimilate CO_2, especially at high CO_2.

(2) *Respiration*

(a) CO_2 *efflux from single stems*. Respiration was determined in excised stem segments of the sedge, *Scirpus olneyi*. Tissues were placed in metal tubes, immersed in a temperature controlled water bath and the net efflux of CO_2 was measured using an infra-red gas analyser as detector (ADC, MK II). Measurements were made at a range of temperatures between 15 and 35°C at the growth CO_2 concentration and in CO_2-free air. Plants grown in elevated CO_2 had a reduced specific respiration rate expressed as the CO_2 efflux per unit dry weight (Drake *et al.* 1989). The data in Table 2 show that there are two effects, one related to the CO_2 concentration during growth and the second related to the concentration during the measurement. In both cases, the respiration rate was reduced whether the CO_2 concentration was increased during measurement or when the rate was compared between tissues grown in different CO_2 concentrations.

Subsequent measurements using an O_2 electrode on pieces of stem tissues from the C_3 plant *Scirpus olneyi* and leaf and stem tissues from the C_4 grass, *Spartina patens*, confirmed that the reduction in the respiration rate, measured as the consumption of oxygen, was reduced from tissues of the C_3 sedge but not from the C_4 grass (Azcón-Bieto and Drake, unpublished). The consumption of O_2 in these experiments was reduced whether the results were expressed on a dry weight or tissue N basis.

Table 2. Effect of growth in elevated CO_2 on dark respiration in
Scirpus olneyi
Data are rates of CO_2 efflux (μmol kg^{-1} s^{-1}; dry weight basis) from
stem tissues in the dark at 26C (Drake *et al.* 1989)

Treatment	CO_2 efflux (μmol kg^{-1} s^{-1}) in:	
	Operational concentration	CO_2-free air
Ambient	1.8	2.3
Elevated	1.2	1.6
E/A	0.67	0.70

(3) Nitrogen

(a) Nitrogen content of tissues. Nitrogen content of the tissues was determined in leaves, stems, flower bracts, roots and rhizomes (Curtis *et al.* 1989*b*). Tissue N content decreased in elevated CO_2 in the C_3 sedge but not in the C_4 grass. The reduction in N content was also observed in the bracts of the reproductive structures of *Scirpus olneyi* but not in the seeds. The decreased N content increased C/N in all tissues and this was expected to have an effect on the rate of decomposition, discussed below.

(b) Nitrogen uptake. Studies of the nitrogen uptake and of nitrogen fixation by plants in the field were carried out in 1990 (Dakora and Drake, unpublished). Acetylene reduction was used to estimate nitrogenase activity in potted whole plants and roots in the field. The C_3 sedge treated with elevated CO_2 showed increased nitrogenase activity, but elevated CO_2 had no such effect on the C_4 plant. In ^{15}N studies in which the labelled substrate was applied to washed roots and excised stems, there was increased assimilation of radiolabelled N in roots of the C_3 sedge grown in elevated CO_2, but there was little activity and no detectable effect of elevated CO_2 on the washed roots from the C_4 grass. These studies clearly show that elevated CO_2 had a profound effect on the nitrogen economy of the plant but it is not clear whether the total available nitrogen in the soil was reduced by the elevated CO_2 treatment.

(4) Biomass production

(a) Shoots. Aboveground biomass production was estimated using a non-destructive method (Curtis *et al.* 1989*a*). In the C_3 sedge community, length of green and dead portions of each shoot and the total number of shoots in each site were determined. In the C_4 grass community, the numbers of shoots in five randomly chosen 10 x 10 cm quadrats in each chamber were counted and the dry weight and number of shoots in five 5 x 5 cm quadrats were determined.

During the first year of treatment, this procedure was carried out seven times in each site, four times the second year and twice for each year thereafter. There was no detectable effect of the elevated CO_2 treatment on above-ground biomass for the first 10 weeks of growth (Curtis *et al.* 1989*a*). After the middle of July, the numbers of shoots in the elevated CO_2 chambers began to increase significantly beyond that in the normal ambient CO_2 treatment. By the end of the season there was a large difference between the treatments. Evidently, the elevated CO_2 treatment caused a delay in senescence of approximately 2 weeks. The elevated CO_2 treatment had no measurable effect on the numbers of shoots or biomass in the C_4 grass community or in the mixed community (discussed below).

The data in Fig. 1 show the shoot density at mid-season during 4 years of elevated CO_2 treatment. The elevated CO_2 treatment produced relatively more *Scirpus olneyi* shoots in the mono-specific stands during the 1987 and 1988 growing seasons than during the 1989 and

1990 growing seasons, which was attributed to the relatively hotter and dryer years of 1987 and 1988 (Arp *et al.* 1992).

(*b*) *Shoot growth rate and anatomy.* The elevated CO_2 treatment had no effect on specific weight (g dm^{-3}) in the C_4 grass although there was a small increase of about 5% in the C_3 sedge (Arp 1991*b*). Similarly, there was no effect of elevated CO_2 on the areas of different cell types measured on cross sections of the shoot in photomicrographs (Table 1). Measurements of *Scirpus olneyi* shoot elongation rates during growth in June and July 1988 showed no difference between the treatments.

(*c*) *Root growth.* The effects of elevated CO_2 on the production of below-ground biomass was estimated from the re-growth of roots and rhizomes into cores which had been removed and re-filled with ground sphagnum peat. The re-growth cores were established prior to the outset of the second year of CO_2 exposure and removed in December after the chambers had been taken from the field plots, a period of 10 months. The roots were separated from the peat matrix, and the biomass in each 5 cm layer was determined (Curtis *et al.* 1990).

There was an 83% stimulation of root biomass caused by the elevated CO_2 treatment in the C_3 *Scirpus olneyi* community but no statistically significant effect on root growth in the pure C_4 community nor in the mixed community.
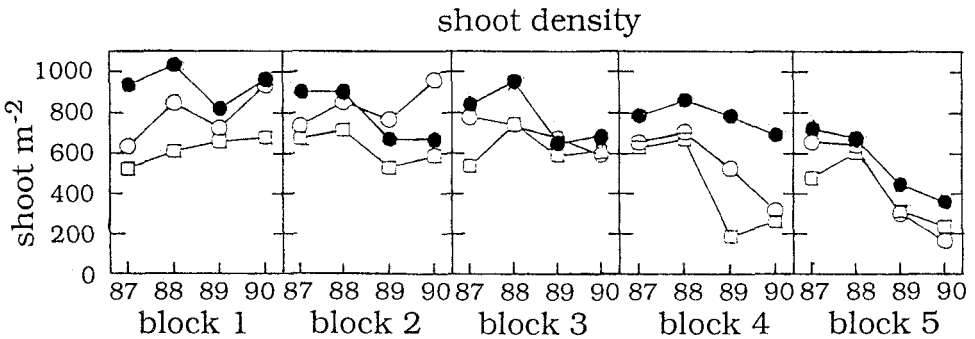

Fig. 1. Shoot density of *Scirpus olneyi* in the C_3 community. Values shown represent peak biomass from 1987 through 1990, for each of the 15 chambers. Open circles represent data from plants grown and measured in normal ambient CO_2; closed circles represent data from plants grown and measured in elevated CO_2; and open squares represent data from plants in the control sites. From Arp (1991*b*).

Ecosystem and Community Responses

(1) Competition

The effect of elevated CO_2 on the relative abundance of the C_3 component of a mixed C_3/C_4 community was determined by comparison of the biomass of each component through 4 years of treatment (Arp *et al.* 1992). Methods for determining the numbers of shoots and biomass were the same as outlined above for the pure C_3 and C_4 communities. Data on the yearly change in the C_3 component of the mixed community are shown in Fig. 2. In the mixed community, the C_3 plant occupies a small fraction of the total biomass at mid-season. In 1989, the mixed community in elevated CO_2 treatment had the following distribution of biomass: 136.7 g for the C_3 sedge, 409 g for the C_4 grass, *Spartina patens*, and 362.9 g for the C_4 grass, *Distichlis spicata*. The C_3 component was thus approximately 15% of the biomass in the elevated CO_2 treatment (908.6 g) but it was only 7% of the total biomass in the normal ambient CO_2 treatment (969.5 g). There was a very large and statistically significant effect of elevated CO_2 on shoot density and total biomass of the C_3 plant and a small but statistically significant decline in the biomass of the C_4 component in the mixed community.
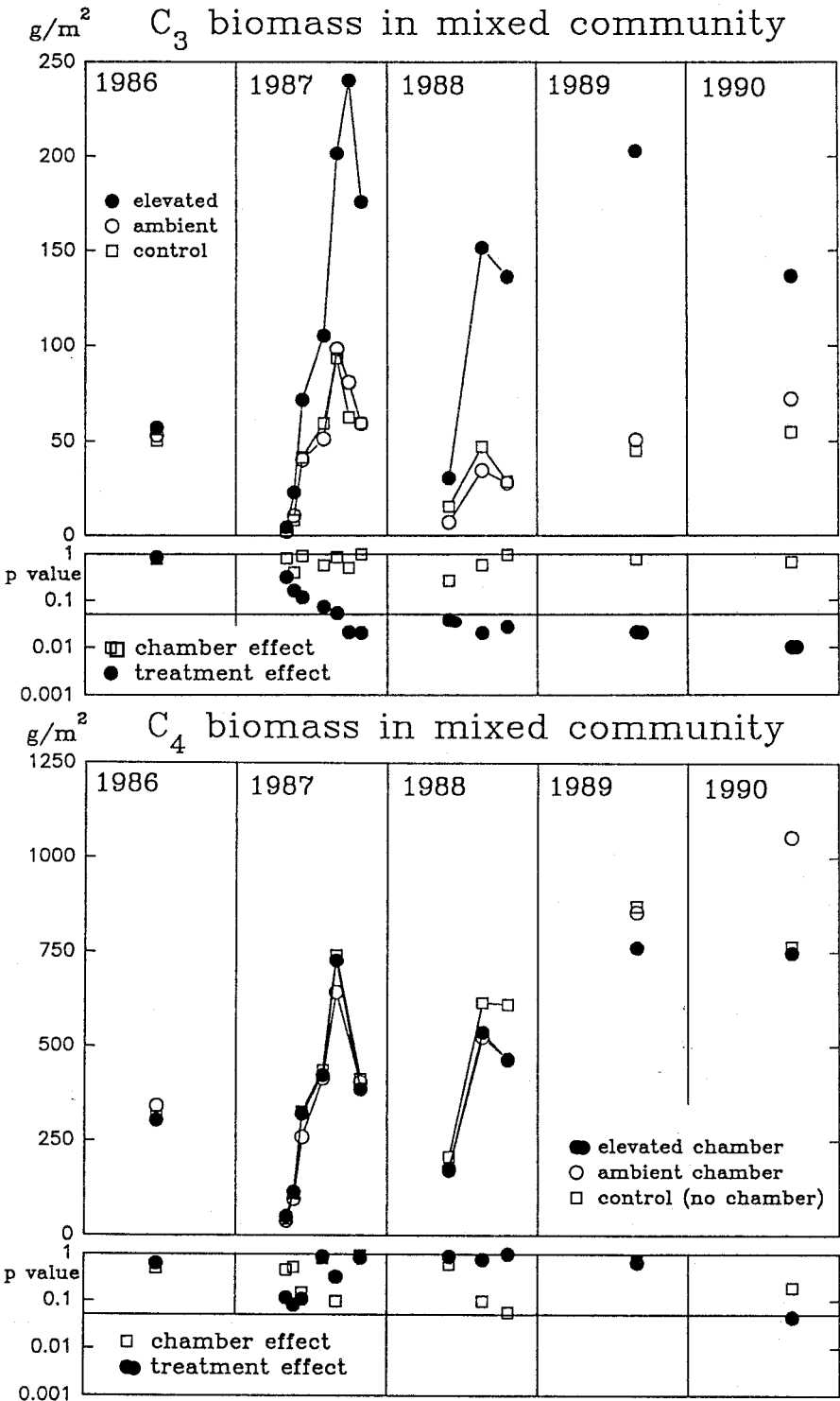
Fig. 2. Total biomass of the C_3 sedge *Scirpus olneyi* and the C_4 grasses *Spartina patens* and *Distichlis spicata* in the mixed community of *Scirpus*, *Spartina*, and *Distichlis* for all harvests from 1986 to 1990. CO_2 treatment started in 1987. Values shown are mean values for 5 chambers. p-values for the difference between elevated and ambient chambers (treatment effect) and between ambient chambers and control sites (chamber effect). The horizontal line represents the 0.05 level.

(2) *Ecosystem NCE and H$_2$O exchange*

(a) *Canopy photosynthesis.* Gas exchange between the air and sections of stands within the open top chambers was determined by converting the open top chamber to a gas exchange cuvette by the addition of a top with a chimney (Drake and Leadley 1991; Leadley and Drake 1992). The difference between gas composition entering and leaving the chamber was measured on samples of air supplied continuously from the inlet and exhaust side of the chambers to the gas analysers and dew-point detectors in the station (Fig. 3). Flow rate through the chamber was determined periodically using a hot wire anemometer (Kurz Instruments, Digital Air Velocity Meter model 1440M). Net CO$_2$ and H$_2$O exchange were determined for each chamber at least twice per month throughout the 4 year period from 1987 through 1990. A representative sample of the diurnal gas exchange data is shown in Fig. 4 after Drake and Leadley (1991).
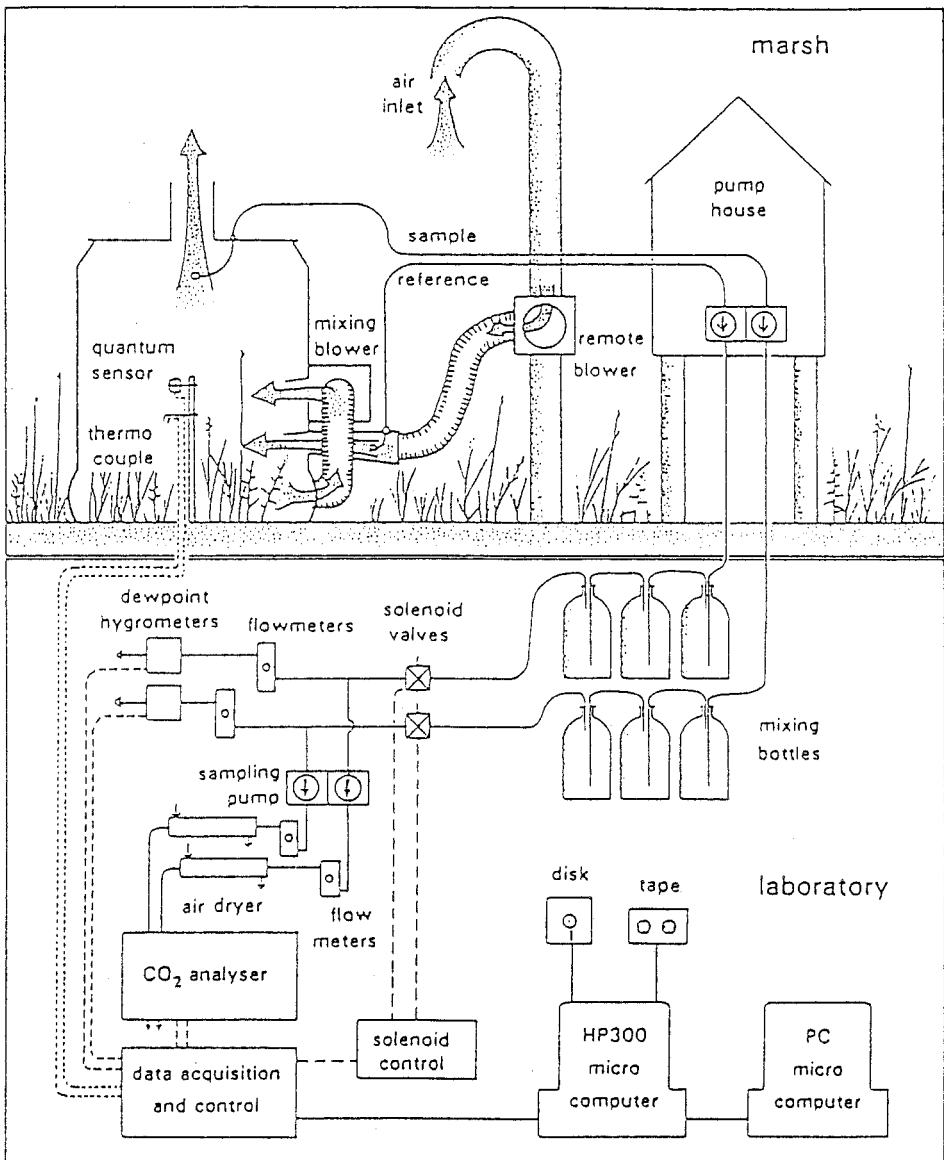
An analysis of data for this period shows a highly significant difference between NCE_a in the pure C_3 *Scirpus olneyi* community for all four years. The effects of elevated CO_2 on ecosystem gas exchange in the mixed and pure C_4 communities, dominated by *Spartina patens*, were statistically significant for only two of the four years. As a result of the increased numbers of green shoots and also as a result of a delay in senescence of the green tissues in the C_3 community (Curtis *et al.* 1989*a*), elevated CO_2 stimulated NCE_a by an amount which increased throughout the season. During the 1988 season the stimulation of NCE_b was virtually constant at approximately 55% (Leadley and Drake, in press). Data for the total carbon budget are shown in Table 3. Elevated CO_2 stimulated carbon accumulation in all three communities but the effect was about 50% greater in the C_3 *Scirpus olneyi* community than in either the pure C_4 *Spartina patens* or mixed communities.
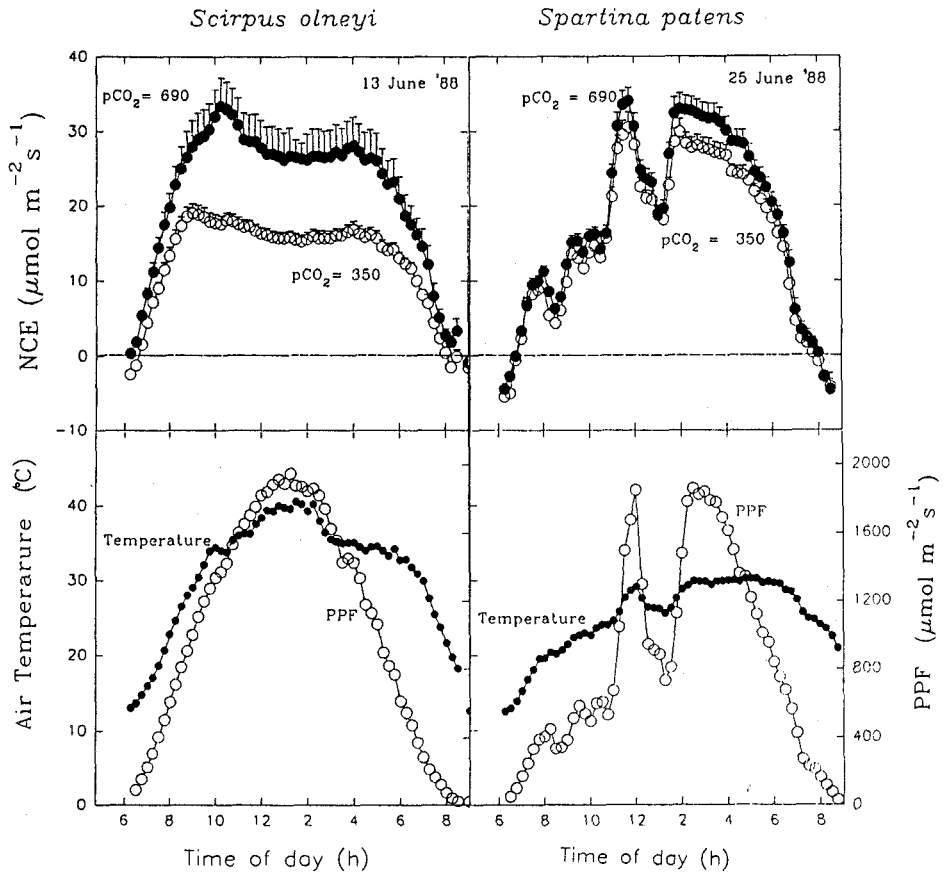

Fig. 4. Net ecosystem CO_2 exchange per unit ground area (NCE_a) in the monospecific C_3 sedge, *Scirpus olneyi*, and in the C_4 grass, *Spartina patens*. Values are means and standard errors for five chambers in each community determined for 15-min intervals throughout the day. Open circles represent data from plants grown and measured in normal ambient CO_2; closed circles represent data from plants grown and measured in elevated CO_2.

Fig. 3. Diagram showing the gas circuit for CO_2 monitoring and chamber gas exchange measurements. The electrical connections for data acquisition and management are also shown (after Arp 1991*b).

(b) *Evapotranspiration*. Water vapour content was determined in the same gas streams with CO_2 concentration by passing a part of the sample gas across a dew point detector (General Eastern, model Dew-10). Net evapotranspiration could not be determined during the early mornings owing to the fact that dew formed on the grass and surfaces of the open top chamber. After approximately 9:30 am on most days, the dew had burned off and realistic data were obtained. Arp (1991b) reported evapotranspiration for the two communities dominated by mono-specific stands of *Scirpus olneyi* and *Spartina patens*. A summary of representative data for ET and WUE is shown in Table 4.

Elevated CO_2 significantly decreased water loss in all years and in both communities by 17-29% which, when combined with the increase in carbon uptake of 18-70%, translated into increased WUE of 72-124% (Table 4). The differences in WUE between years and between communities were due primarily to effects of elevated CO_2 on carbon assimilation which appear to have been determined in large part by climate variables which varied from year to year (Arp *et al.* 1992).

(3) *Plant–microbe and plant–insect interactions*

The effect of elevated CO_2 on infestation by insects and infection by fungi was surveyed during the summer of 1991. Randomly selected stems of *Scirpus olneyi* were removed from each chamber and unchambered companion plot. These were then examined for visual signs of insect damage and for fungal decay. A brief summary of the results of this work extracted from Thompson and Drake (unpublished) is shown in Fig. 5.

Insect damage occurred in a significantly higher number of shoots from the chamberless controls and the normal ambient chambers than from plants grown in elevated CO_2. Similarly, there was less fungal damage in stems from the elevated CO_2 treatment than from the other two treatments.

Table 3. Annual carbon budget for the pure communities dominated by *Scirpus olneyi* and *Spartina patens*

Values are integrated seasonal data for daytime uptake less night-time loss for the year 1990

Community	NCE ($kg\ m^{-2}\ year^{-1}$)		E/A
	Ambient	Elevated	
Scirpus olneyi	3.56	5.51	1.55
Spartina patens	2.97	3.84	1.29
Mixed	2.49	3.47	1.39

Discussion

Many of the results presented in this paper might be predicted from the known responses of plants to elevated CO_2. Evapotranspiration was reduced resulting in increased water potential and WUE in both types of species (Arp 1991b); photosynthesis was increased in the C_3 plant but not in the C_4 species (Ziska *et al.* 1990; Long and Drake 1991). Both root and shoot growth increased in the elevated CO_2 treatment in the C_3 species and the relative effect on root growth was greater than the relative effect on shoot growth (Curtis *et al.* 1989a, 1990); in the mixed community the C_3 plants increased relative to the C_4 plants (Arp *et al.* 1992); nitrogen concentration decreased and the C/N increased in the C_3 but not the C_4 plant (Curtis *et al.* 1989b). These effects essentially confirm the basis for the expected response of vegetation to rising atmospheric CO_2 as determined by a great many studies from greenhouse and controlled environment experiments.

However, some results obtained in this study differ from the results obtained in controlled environments in the following unexpected ways: photosynthetic capacity increased (Arp and

Drake 1991); water loss per unit ground are was reduced (Arp 1991b); dark respiration was reduced in the C_3 sedge, *Scirpus olneyi* (Drake et al. 1989); nitrogen fixation increased in the C_3 but not the C_4 species (Dakora and Drake, unpublished); and herbivory by insects and fungi decreased (Thompson and Drake, unpublished).

Table 4. The effect of elevated CO_2 on NCE, ET and WUE for the two years 1989 and 1990 for mono-specific stands of the C_3 sedge, *Scirpus olneyi*, and the C_4 grass, *Spartina patens*
After Arp (1991b). Mean values for the ratio E/A, ratio of the rate in elevated CO_2 to that in normal ambient CO_2, are based on the mean of five chambers in each treatment computed for the period 1300-1600 hours each day. The number of days used in each analysis is shown in the column after the year. Data which differ significantly in each column at the $P = 0.05$ level are indicated by different letters

| Species | | Ratio E/A | | |
Year (n)		ET	NCE	WUE
Scirpus olneyi				
1988	(10)	0.78 (0.042)[a]	1.70 (0.051)[a]	2.24(0.15)[a]
1989	(9)	0.83 (0.024)[ab]	1.42 (0.036)[b]	1.72(0.04)[a]
Spartina patens				
1988	(7)	0.72(0.028)[a]	1.29 (0.031)[c]	1.91(0.14)[a]
1989	(11)	0.71 (0.28)[ac]	1.18 (0.018)[d]	1.77(0.08)[a]

The effects of elevated CO_2 on growth arise primarily from the increase in photosynthesis. In this study, there was good correlation between the stimulation of carbon exchange at the leaf level and increased biomass production, during the first 2 years of the experiment (Curtis et al. 1989a). The effects of elevated CO_2 can be classified as short-term or kinetic in which the immediate effects of changing CO_2 concentration are limited to the increased rate of gas exchange, and long-term effects in which the CO_2 enriched atmosphere alters molecular components of plant metabolism and/or plant anatomy. Short-term effects of elevated CO_2 increase photosynthesis in C_3 plants but usually does not alter photosynthesis substantially in C_4 plants. When the ambient CO_2 concentration is doubled, the rate of C_3 photosynthesis increases by 15-70% depending on temperature (Long 1991). In some experiments lasting many weeks, the initial high response of photosynthesis declines (Cure and Acock 1986). The results from many long-term elevated CO_2 exposure studies suggest that the long-term response of photosynthesis to rising CO_2 will not be as great as might be expected from the short-term response in single leaves, owing mainly to a reduction in the capacity for CO_2 assimilation as a result of source/sink interactions (Stitt 1991). Observations of the acclimation of photosynthesis in plants exposed to long-term CO_2 treatment has given rise to the expectation that plants will not show much response to elevated CO_2 after an initial burst of growth (Oechel and Strain 1985) in part because biomass production is limited by nutrient supply or environmental stresses such as drought and low temperature. But not all long-term studies report reduction of photosynthetic capacity, and in some studies, photosynthetic capacity is increased (Conroy 1989; Arp and Drake 1991). In cotton, elevated CO_2 exposure resulted in reduction of photosynthetic capacity in one case (DeLucia et al. 1985), reversible reduction of photosynthetic capacity in another (Sasek et al. 1985) and no effect in a third study (Radin et al. 1987).

It has recently been suggested that laboratory studies are often performed with plants in pots small enough to confine the rooting system, and that this condition reduces root growth and results in inhibition of many of the responses to elevated CO_2 including down-regulation of photosynthesis (Arp 1991a). In contrast with controlled environment studies, field

responses of photosynthesis and production are often much greater and usually accompanied by no reduction of photosynthetic capacity (sometimes called 'acclimation' response) or even an increase in the photosynthetic capacity. In addition to the responses reported in this study, the following studies have reported increased photosynthetic capacity after long-term exposure to elevated CO_2: Campbell et al. (1988); Conroy (1989); Sage et al. (1989); Chen and Sung (1990). Examples of reports showing no effect of long-term treatment include Radin et al. (1987) and Sage et al. (1989).

Reduced photosynthetic capacity has been reported by Wong (1979, 1980); Downton et al. (1980); Kriedemann and Wong (1984); von Caemmerer and Farquhar (1984); DeLucia et al. (1985); Ehret and Jolliffe (1985); Tissue and Oechel (1987); Sage et al. (1989) and Thomas and Strain (1991). Experimental manipulation of pot size and of fruits has been used to test the interacting effects of sink size with elevated CO_2. These studies have shown that photosynthetic capacity can be regulated by changing sink size in the presence of elevated CO_2 (Clough et al. 1981; Thomas and Strain 1991).
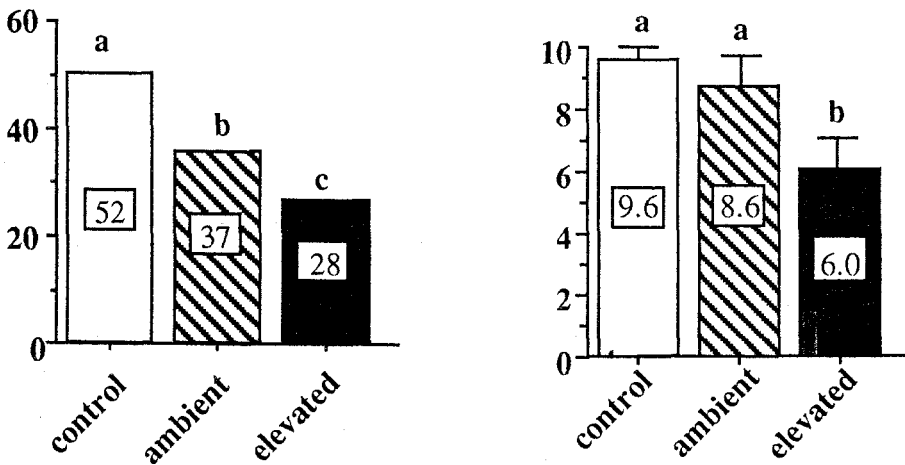

Fig. 5. The mean % leaf area covered by fungi (left) and the incidence of insect infestation (right) on *Scirpus olneyi*. Bars are means with standard errors. Different letters indicate that means are significantly different at the 0.05 level. Numbers in bars are means. Data after Thompson and Drake (unpublished).

It is not clear whether or how environmental conditions that exist in the field promote reduction of photosynthetic capacity in response to elevated CO_2. Only one study has so far shown this response. In *Eriophorum vaginatum*, an Arctic tussock tundra species, photosynthesis of plants grown in elevated CO_2 was the same as that of plants grown in normal ambient CO_2 concentration within 3 weeks after exposure to elevated CO_2 when compared at the respective operating concentrations (Tissue and Oechel 1987).

The importance of the response of photosynthesis to the multiple effects of the elevated CO_2 treatment in this study is emphasised by the data in Table 5. Overall, carbon sequestering increased in the C_3 community dominated by *Scirpus olneyi* as a result of a number of interacting factors including: increased quantum yield and photosynthetic capacity and decreased light compensation point of individual shoots; increased leaf area; delayed senescence; improved water balance; and decreased dark respiration.

Table 5. Effect of elevated CO_2 on plant and ecosystem processes
Elevated CO_2 treatment decreases (-), increases (+),
or has no effect (0) on the process

Category	Scirpus C_3	Spartina C_4
Evapotranspiration	-	-
Stem water potential	+	+
Photosynthesis	+	0
Shoot number	+	0
Relative root growth	+	0
Nitrogenase activity	+	0
Nitrogen fixation	+	0
Nitrogen concentration	-	0
Senescence	-	0
Decomposition	-	0
Methane production	+	0

A surprising finding of this study was the decrease in dark respiration of the C_3 sedge, *Scirpus olneyi* (Table 2). The data in this table show that in *Scirpus olneyi* the response consists of at least two components, a short-term or kinetic response and a long-term reduction in dark respiration. Both types of response of dark respiration to elevated CO_2 have been reported. Short-term responses have been reported by Kidd (1916), Nilovskaya and Razoryonova (1968), Bunce (1990) and Amthor (1991). Long-term responses measured by comparing the response of grown in elevated CO_2 with plants grown in present normal ambient CO_2 are reported in the studies by Ludwig *et al.* (1975), Gifford *et al.* (1985), Reuveni and Gale (1985), Spencer and Bowes (1986), Allen *et al.* (1989) and Bunce (1990). It may be that the response is dependent on the growth stage of the plant. We found that there was no apparent effect of the elevated CO_2 treatment on dark respiration until mid-June which is almost 8 weeks after the beginning of the CO_2 treatment (Drake *et al.* 1989). Some reports showing increased respiration in elevated CO_2 are measured on rapidly expanding leaves (Hrubec *et al.* 1985; Poorter *et al.* 1988).

There have been few attempts to test the various possible scenarios which emerge from a consideration of the above facts, including the possibility that elevated CO_2 will increase production with increased photosynthetic capacity, that downregulation of photosynthesis will limit production, or that biomass production in aboveground tissues will be limited but that photosynthesis will be stimulated in native ecosystems.

The largest responses of plants to elevated CO_2 occur in the presence of environmental stress (Cure and Acock 1986). In our study it is surprising that there is so little effect of elevated CO_2 in the apparent relief of water and salt stress. Although there was a clear increase in water potential both at dawn and midday in all three species (Arp 1991*b*), the only evidence that this had any effect was a small but significant increase in the net ecosystem CO_2 exchange in the pure C_4 grass community dominated by *Spartina patens*.

There have been seven studies of canopy photosynthesis of plants grown in elevated atmospheric CO_2: three of seed crops, two of forage crops and two of native plant ecosystems (Jones *et al.* 1984, 1985*a*, 1985*b*; Acock *et al.* 1985; Oechel and Strain 1985; Overdieck and Lieth 1986; Tissue and Oechel 1987; Nijs *et al.* 1988; Allen *et al.* 1989; Grulke *et al.* 1990; Drake and Leadley 1991). Growth in elevated CO_2 increased canopy photosynthesis in all cases. The relative effect of CO_2 was correlated with increasing temperature: the least stimulation occurred in tundra vegetation grown at an average temperature near 10ºC and the greatest in rice grown at 43ºC. In soybean, effects of CO_2 were greater during leaf expansion and pod fill than at other stages of crop maturation.

The results of the Arctic tundra study showed that elevated CO_2 stimulated photosynthesis (Grulke *et al.* 1990), even though there was complete homeostatic adjustment of assimilation of single-leaf rates in the dominant species, *Eriophorum vaginatum*, after 3 weeks of exposure to elevated CO_2 (Tissue and Oechel 1987). The explanation appears to be due to at least two factors: first, *Eriophorum* showed considerable tillering in elevated CO_2, and second, there were a number of species other than *Eriophorum* which may not have acclimated. The combined effects may have accounted for the majority of the uptake of CO_2. It is hard to find in their data the justification for the claim by Grulke *et al.* (1990) that there would be '...little if any long-term increase in carbon acquisition by increased atmospheric CO_2'.

Canopy photosynthesis in a mixture of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) in Osnabruck, Germany, increased 25-45% in 600 ppm CO_2 compared to 340 ppm CO_2 (Overdieck and Lieth 1986).

Herbivory and fungal infection were both reduced in the C_3 community in elevated CO_2 (Thompson and Drake, unpublished). In this study, the distribution of insect larvae correlated with reduced nitrogen in the tissues and this was true within and among the various chambers. This observation is not consistent with other feeding studies in which the usual finding is that herbivory is increased when insects are fed on tissues from elevated CO_2 treatments (Lincoln *et al.* 1986; Fajer *et al.* 1989), although some reports showed increased ingestion from both higher and lower than normal ambient CO_2 treatments (Johnson and Lincoln 1990). It appears that, if insects have a choice, they prefer tissue richest in nitrogen. Whether this has any meaning for plants growing in a higher CO_2 world is not clear.

Acknowledgments

References

Acock, B., Reddy, V.R., Hodges, H.F., Baker, D.N,. and McKinion, J.M. (1985). Photosynthetic response of soybean canopies to full-season carbon dioxide enrichment. *Agronomy Journal* **77,** 942-47.

Allen, L.H. Jr., Boote, K.J., Jones, P.H., Jones, J.W., Rowland-Bamford, A.J., Bowes, G., Graetz, D.A., and Reddy, K.R. (1989). 'Temperature and CO_2 Effects on Rice: 1988.' (United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division: Washington, D.C.)

Amthor, J.S. (1991). Respiration in a future, higher-CO_2 world. *Plant, Cell and Environment* **14,** 13-20.

Arp, W.J. (1991*a*). Effects of source–sink relations on photosynthetic acclimation to elevated CO_2. *Plant, Cell and Environment* **14,** 869-75.

Arp, W.J. (1991*b*). Vegetation of a North American salt marsh and elevated atmospheric carbon dioxide. Doctoral Thesis, Free University of Amsterdam.

Arp, W.J., and Drake, B.G. (1991). Increased photosynthetic capacity of *Scirpus olneyi* after 4 years of exposure to elevated CO_2. *Plant, Cell and Environment* **14,** 1003-06.

Arp, W.J., Drake, B.G., Pockman, W.T., Curtis, P.S., and Whigham, D.F. (1992). Effects of four years exposure to elevated atmospheric CO_2 on competition between C_3 and C_4 salt marsh plant species. *Vegetatio* (in press).

Bunce, J.A. (1990) Short and long term inhibition of respiratory carbon dioxide efflux by elevated carbon dioxide. *Annals of Botany* **65,** 637-42.

Campbell, W.J., Allen, L.H. Jr., and Bowes, G. (1988). Effects of CO_2 concentration on rubisco activity, amount, and photosynthesis in soybean leaves. *Plant Physiology* **88,** 1310-16.

Chen, J.J., and Sung, J.M. (1990). Gas exchange rate and yield responses of Virginia-type peanut to carbon dioxide enrichment. *Crop Science* **30,** 1085-89.

Clough, J.M., Peet, M.M., and Kramer, P.J. (1981). Effects of high atmospheric CO_2 and sink size on rates of photosynthesis of a soybean cultivar. *Plant Physiology* **67,** 1007-10.

Conroy, J. (1989). Influence of high CO_2 on *Pinus radiata*. Ph.D. Thesis, Macquarie Unversity.

Cure, J.D., and Acock, B. (1986) Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology* **38,** 127-45.

Curtis, P.S., Drake, B.G., and Whigham, D.F. (1989*b*). Nitrogen and carbon dynamics in C_3 and C_4 estuarine marsh plants grown under elevated CO_2 in situ. *Oecologia* **78,** 297-301.

Curtis, P.S., Balduman, L.M., Drake, B.G., and Whigham, D.F. (1990). Elevated atmospheric CO_2 effects on belowground processes in C_3 and C_4 estuarine marsh communities. *Ecology* **71,** 2001-06.

Curtis, P.S., Drake, B.G., Leadley, P.W., Arp, W.J., and Whigham, D.F. (1989*a*) Growth and senescence in plant communities exposed to elevated CO_2 concentrations on an estuarine marsh. *Oecologia* **78,** 20-26.

DeLucia, E.H., Sasek, T.W., and Strain, B.R. (1985). Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosynthesis Research* **7,** 175-84.

Downton, W.J.S., Björkman, O., and Pike, C.S. (1980) Consequences of increased atmospheric concentrations of carbon dioxide for growth and photosynthesis of higher plants. In 'Carbon Dioxide and Climate: Australian Research'. (Ed. G.I. Pearman.) pp. 143-51. (Australian Academy of Science: Canberra.)

Drake, B.G., and Leadley, P.W. (1991). Canopy photosynthesis of crops and native plant communities exposed to long-term elevated CO_2. *Plant, Cell and Environment* **14,** 853-60.

Drake, B.G., Leadley, P.W., Arp, W.J., Nassiry, K., and Curtis, P.S. (1989). An open top chamber for field studies of elevated atmospheric CO_2 concentration on saltmarsh vegetation. *Functional Ecology* **3,** 363-71.

Drake, B.G., Arp, W., Craig, J., Curtis, P.S., Leadley, P.W., and Whigham, D.F. (1987). 'Effects of Elevated CO_2 on Chesapeake Bay Wetlands. II. Gas Exchange and Microenvironment in Open Top Chambers.' (United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division: Washington, D.C.)

Drake, B.G., Curtis, P.S., Arp, W.J., Leadley, P.W., Johnson, J., and Whigham, D.F, (1988). 'Effects of Elevated CO_2 on Chesapeake Bay Wetlands. III. Ecosystem and Whole Plant Responses in the First Year of Exposure, April–November 1987.' (United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division: Washington, D.C.)

Drake, B.G., Arp, W.J., Balduman, L., Curtis, P.S., Johnson, J., Kabara, D., Leadley, P.W., Pockman, W.T., Seliskar, D., Sutton, M.L., Whigham, D.F,, and Ziska, L. (1989). 'Effects of Elevated CO_2 on Chesapeake Bay Wetlands. IV. Ecosystem and Whole Plant Responses. April–November 1988.' (United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division: Washington, DC.)

Eamus, D., and Jarvis, P.G. (1989). The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research* **19,** 1-55.

Ehret, D.L., and Jolliffe, P.A. (1985). Photosynthetic carbon dioxide exchange of bean plants grown at elevated carbon dioxide concentrations. *Canadian Journal of Botany* **63,** 2026-30.

Fajer, E.D., Bowers, M.D., and Bazzaz, F.A. (1989). The effects of enriched carbon dioxide atmospheres on plant–insect herbivore interactions. *Science* **243,** 1198-1200.

Gifford, R.M., Lambers, H., and Morison, J.I.L. (1985). Respiration of crop species under CO_2 enrichment. *Physiologia Plantarum* **63,** 351-56.

Grulke, N.E., Rieckhers, G.H., Oechel, W.C., Hjelm, U., and Jaeger, C. (1990). Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. *Oecologia* **83,** 485-94.

Houghton, J.T., Jenkins, G.J., and Ephraums, J.J. (1990). 'Climate Change. The IPCC Scientific Assessment.' (Cambridge University Press: Cambridge.)

Houghton, R.A., and Woodwell, G.M. (1989). Global climatic change. *Scientific American* **260,** 36-44.

Houghton, R.A., Boone, R.D., Melillo, J.M., Palm, C.A., Woodwell, G.M., Myers, N., and Moore, B. III (1985). Net flux of carbon dioxide from tropical forests in 1980. *Nature* **316,** 617-20.

Hrubec, T.C., Robinson, J.M., and Donaldson, R.P. (1985). Effects of CO_2 enrichment and carbohydrate content on the dark respiration of soybeans. *Plant Physiology* **79,** 684-89.

Idso, S.B., Kimball, B.A., and Allen, S.G. (1991). Net photosynthesis of sour orange trees maintained in atmospheres of ambient and elevated CO_2 concentration. *Agricultural and Forest Meteorology* **54,** 95-101.

Ireland, C.R., Long, S.P., and Baker, N.R. (1989). An integrated portable apparatus for the simultaneous field measurement of photosynthetic CO_2 and water vapour exchange, light absorption and chlorophyll fluorescence emission of attached leaves. *Plant, Cell and Environment* **12,** 947-58.

Johnson, R.H., and Lincoln, D.E. (1990). Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. *Oecologia* **84,** 103-10.

Jones, P., Allen, L.H. Jr., and Jones, J.W. (1985a) Responses of soybean canopy photosynthesis and transpiration to whole day temperature changes in different CO_2 environments. *Agronomy Journal* **77**, 242-49.

Jones, P., Allen, L.H. Jr., Jones, J.W., and Valle, R. (1985b) Photosynthesis and transpiration responses of soybean canopies to short-and long-term CO_2 treatments. *Agronomy Journal* **77**, 119-26.

Jones, P.H., Allen, L.H. Jr., Jones, J.W., Boote, K.J., and Campbell, W.J. (1984). Soybean canopy growth, photosynthesis, and transpiration responses to whole-season carbon dioxide enrichment. *Agronomy Journal* **76**, 633-37.

Jordan, D., and Ogren, W.L. (1984). The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase dependence on ribulosebisphosphate concentration, pH and temperature. *Planta* **161**, 308-13.

Kidd, F. (1916). The controlling influence of carbon dioxide. Part III. The retarding effect of carbon dioxide on respiration. *Proceedings of the Royal Society of London, Series B* **89**, 136-56.

Kimball, B.A. (1983). Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**, 779-88.

Kriedemann, P.E., and Wong, S.C. (1984) Growth response and photosynthetic acclimation to CO_2: comparative behavior in two C_3 crop species. *Acta Horticulturae* **162**, 113-20.

Leadley, P.W., and Drake, B.G. (1992). Open top chambers for exposing plant canopies to elevated CO_2 concentration and for measuring net gas exchange. *Vegetatio* (in press).

Lincoln, D.E., Couvet, D., and Sionit, N. (1986). Response of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia* **69**, 556-60.

Lindzen, R.S. (1992). Global warming: the origin and nature of alleged scientific consensus. In 'OPEC Seminar on the Environment'. pp.157-71.

Long, S.P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: has its importance been underestimated? *Plant, Cell and Environment* **14**, 729-39.

Long, S.P., and Drake, B.G. (1991). Effect of the long-term elevation of CO_2 concentration in the field on the quantum yield of photosynthesis of the C_3 sedge, *Scirpus olneyi*. *Plant Physiology* **96**, 221-26.

Long, S.P., and Drake, B.G. (1992). Photosynthetic CO_2 assimilation and rising atmospheric CO_2 concentrations. In 'Crop Photosynthesis: Spatial and Temporal Determinants'. (Eds N.R. Baker and H. Thomas.) (Elsevier Science Publishers: Amsterdam.) (In press.)

Lorimer, G.H. (1981). The carboxylation and oxygenation of ribulose 1,5-bisphosphate: the primary events in photosynthesis and photorespiration. *Annual Review of Plant Physiology* **32**, 349-83.

Ludwig, R., Charles-Edwards, D.A., and Withers, A.C. (1975) Tomato leaf photosynthesis and respiration in various light and carbon dioxide environments. In 'Environmental and Biological Control of Photosynthesis'. (Ed. R. Marcelle.) pp. 29-36. (W. Junk: The Hague.)

Nijs, I., Impens, I., and Behaeghe, T. (1988). Leaf and canopy responses of *Lolium perenne* to long-term elevated atmospheric carbon-dioxide concentration. *Planta* **177**, 312-20.

Nilovskaya, N.T., and Razoryonova, T.A. (1968). Respiration rate of vegetable plants at various partial pressures of carbon dioxide. *Fiziologiya Rastenii* **5**, 876-83.

Oechel, W.C., and Strain, B.R. (1985). Native species responses to increased atmospheric carbon dioxide concentration. In 'Direct Effects of Increasing Carbon Dioxide on Vegetation'. (Eds B.R. Strain and J.D. Cure.) pp. 117-54. (United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division: Washington, D.C.)

Overdieck, D. (1990). Direct effects of elevated CO_2 concentration levels on grass and clover in 'model ecosystems'. In 'Expected Effects of Climatic Change on Marine Coastal Ecosystems'. (Eds J.J. Beukema, W.J. Wolff and J.J.W.M. Brouns.) pp. 41-47. (Kluwer Academic Publishers: Dordrecht.)

Overdieck, D., and Lieth, H. (1986). Final report of the project: Long-term effects of increased atmospheric CO_2 concentration level on terrestrial plants in model-ecosystems. Universitat Osnabruck, Fachbereich Biologie/Chemie, Arbeitsgruppe Okologie, Osnabruck.

Poorter, H., Pot, S., and Lambers, H. (1988). The effect of an elevated atmospheric CO_2 concentration on growth, photosynthesis and respiration of *Plantago major*. *Physiologia Plantarum* **73**, 553-59.

Radin, J.W., Kimball, B.A., Hendrix, D.L., and Mauney, J.R. (1987). Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field. *Photosynthesis Research* **12**, 191-203.

Reuveni, J., and Gale, J. (1985). The effect of high levels of carbon dioxide on dark respiration and growth of plants. *Plant, Cell and Environment* **8**, 623-28.

Sage, R.F., Sharkey, T.D., and Seemann, J.R. (1989). Acclimation of photosynthesis to elevated CO_2 in five C_3 species. *Plant Physiology* **89**, 590-96.

Sasek, T.W., DeLucia, E.H., and Strain, B.R. (1985). Reversibility of photosynthetic inhibition in cotton after long-term exposure to elevated CO_2 concentrations. *Plant Physiology* **78**, 619-22.

Shaver, G.R., Hobbie, J.F., Houghton, R.A., Mellilo, J.M., Moore, B., Peterson, B.J., and Woodwell, G.M. (1982). The role of terrestrial biota and soils in the global carbon budget. In 'Global Dynamics of Biosphere Carbon'. (Ed. S. Brown.) pp. 160-65. (US Department of Energy: Washington, D.C.)

Singer, S.F., Revelle, R., and Starr, C. (1991). What to do about greenhouse warming: look before you leap. *Cosmos,* 28-33.

Spencer, W., and Bowes, G. (1986). Photosynthesis and growth of water hyacinth under CO_2 enrichment. *Plant Physiology* **82**, 528-33.

Stitt, M. (1986). Limitation of photosynthesis by carbon metabolism. I. Evidence for excess electron transport capacity in leaves carrying out photosynthesis in saturating light and CO_2. *Plant Physiology* **81**, 1115-22.

Stitt, M. (1991). Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell and Environment* **14**, 741-62.

Thomas, R.B., and Strain, B.R. (1991). Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiology* **96**, 627-34.

Tissue, D.T., and Oechel, W.C. (1987). Response of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan tussock tundra. *Ecology* **68**, 401-10.

von Caemmerer, S., and Farquhar, G.D. (1984). Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. *Planta* **160**, 320-29.

Wong, S.C. (1979). Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. *Oecologia* **44**, 68-74.

Wong, S.C. (1980). Effects of elevated partial pressure of CO_2 on rate of CO_2 assimilation and water use efficiency in plants. In 'Carbon Dioxide and Climate: Australian Research'. (Ed. G.I. Pearman.) pp. 159-66. (Australian Academy of Science: Canberra.)

Woodwell, G.M. (1978). The carbon dioxide question. Can forests and the ocean take up enough carbon to forestall a possible change in world climate? *Scientific American* **238**, 34-43.

Woodwell, G.M., Whittaker, R.H., Reiners, W.A., Likens, G.E., Delwiche, C.C., and Botkin, D.B. (1978). The biota and the world carbon budget. *Science* **199**, 141-46.

Ziska, L.H., Drake, B.G., and Chamberlain, S. (1990). Long-term photosynthetic response in single leaves of a C_3 and C_4 salt marsh species grown at elevated atmospheric CO_2 *in situ*. *Oecologia* **83**, 469-72.