

COMMISSIONED REVIEW

Canopy photosynthesis of crops and native plant communities exposed to long-term elevated CO₂

B. G. DRAKE & P. W. LEADLEY* Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037, U.S.A.

Received 28 May 1991

Abstract. There have been seven studies of canopy photosynthesis of plants grown in elevated atmospheric CO₂: three of seed crops, two of forage crops and two of native plant ecosystems. Growth in elevated CO₂ increased canopy photosynthesis in all cases. The relative effect of CO₂ was correlated with increasing temperature: the least stimulation occurred in tundra vegetation grown at an average temperature near 10°C and the greatest in rice grown at 43°C. In soybean, effects of CO₂ were greater during leaf expansion and pod fill than at other stages of crop maturation. In the longest running experiment with elevated CO₂ treatment to date, monospecific stands of a C₃ sedge, *Scirpus olneyi* (Grey), and a C₄ grass, *Spartina patens* (Ait.) Muhl., have been exposed to twice normal ambient CO₂ concentrations for four growing seasons, in open top chambers on a Chesapeake Bay salt marsh. Net ecosystem CO₂ exchange per unit green biomass (NCE_b) increased by an average of 48% throughout the growing season of 1988, the second year of treatment. Elevated CO₂ increased net ecosystem carbon assimilation by 88% in the *Scirpus olneyi* community and 40% in the *Spartina patens* community.

Key-words: elevated CO₂; canopy photosynthesis; ecosystem carbon budget; unmanaged ecosystems; gas exchange; C₃ and C₄.

Introduction

Will rising atmospheric CO₂ increase ecosystem carbon assimilation? Biomass production usually increased in plants grown in elevated CO₂ compared to those grown in normal ambient CO₂ (Cure, 1985; Cure & Acock, 1986; Kimball, 1983) but in many experiments photosynthetic capacity gradually declined during long-term exposure (Delucia, Sasek & Strain, 1985; Kramer, 1981; Percy & Bjorkman, 1983; Tissue & Oechel, 1987; Cure & Acock, 1986). This has been interpreted to mean that environmental factors which limit growth, such as nutrient availability, will ultimately result in reduced photosynthetic capacity and decrease the capacity of unmanaged ecosystems to accumulate additional carbon

(Goudriaan & Ajtay, 1979; Jarvis, 1989; Kramer, 1981; Oechel & Strain, 1985). This speculation is based on data from plants grown in controlled environments or in greenhouses. Many of these studies were done with annual plants having relatively low capacity for carbon storage and few papers have examined the responses of canopy or ecosystem carbon accumulation. This paper will review those studies in which canopy photosynthesis was determined on swards or small sections of the whole ecosystem exposed to long-term elevated CO₂ treatment. The paper also includes previously unpublished data from a study of the long-term effects of elevated CO₂ treatment on two communities of salt marsh vegetation.

Previous field studies of elevated CO₂ effects on canopy photosynthesis

There have been two studies of soybean canopy photosynthesis (Acock & Allen, 1985; Jones, Allen & Jones, 1985a; Jones *et al.*, 1985b; Jones *et al.*, 1984); a study of canopy photosynthesis in rice (Allen *et al.*, 1989); a study of ryegrass (Nijs, Impens & Behaeghe, 1988); a study of net ecosystem CO₂ exchange (NCE) with 'model-ecosystems' using meadow fescue (*Festuca pratensis* L.) and red clover (*Trifolium pratense* L.; Overdieck & Lieth, 1986); a study in which NCE was measured in the Arctic tussock tundra (Grulke *et al.*, 1990; Oechel & Strain, 1985); and a study of a mesohaline wetland community which is the subject of the latter half of this paper. In all, except for the study of the salt marsh reported here, closed chambers were used. In these, temperature, humidity and CO₂ concentration were controlled in an outdoor setting. The reader is referred to the papers on these studies for details of the chamber design and operation which should be considered when evaluating the results presented. In addition to the above-mentioned studies in which canopy photosynthesis was measured, there have also been other field studies of the photosynthetic properties of soybean (Ackerson, Havelka & Boyle, 1984; Havelka *et al.*, 1984; Sionit *et al.*, 1984) and of cotton (Kimball, 1983; Mauney *et al.*, 1979; Radin *et al.*, 1987) exposed to elevated CO₂ throughout the growing season in the field in open top chambers.

Acock *et al.* (1985a,b) reported that canopy photosyn-

*Present address: Department of Land, Air and Water Resources, University of California, Davis, California 95616, U.S.A.

Correspondence: Bert G. Drake, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037, U.S.A.

thesis of soybean grown in elevated CO₂ was always higher than canopy photosynthesis for soybean in normal ambient CO₂; the relative effect depended on the developmental stage of the crop. During the week when pods began filling, the ratio of photosynthesis in elevated CO₂ (=800 parts of CO₂ per million volumes of air: ppm \equiv cm³ m⁻³) to photosynthesis in normal ambient CO₂ rose from 1.25 to 1.85 and then returned to 1.25 within the following week. Elevated CO₂ increased canopy photosynthesis throughout the growth cycle of soybean and not just during the production of flowers or filling of pods. Jones *et al.* (1984) reported that at 70 d after planting, well past the time of pod filling, maximum photosynthesis in a soybean canopy grown in 800 cm³ m⁻³ CO₂ was 1.70 times the photosynthesis in a canopy of plants grown in 300 cm³ m⁻³.

The response of photosynthesis in single leaves to elevated CO₂ is temperature dependent (Percy & Bjorkman, 1983). See also the opinion paper by S.P. Long in this issue (pp. 729–739) for an analysis of the temperature dependence of the response of photosynthesis to elevated CO₂. This effect, which is due in large part to the temperature dependent specificity of Rubisco for CO₂ (Jordan & Ogren, 1984), suggests that plants growing in widely different temperature regimes should have different responses to CO₂. Measurements of canopy photosynthesis in elevated CO₂ and in different temperature regimes are consistent with this hypothesis. The response of canopy photosynthesis in study of the Arctic tussock tundra appears to have been small but significant nevertheless (Grulke *et al.*, 1990; Oechel & Strain, 1985). Canopy photosynthesis in a mixture of meadow fescue and red clover in a study of model ecosystems in Osnabruck, Germany, increased 25–45% in 600 cm³ m⁻³ CO₂ compared to 340 cm³ m⁻³ (Overdieck & Lieth, 1986). Canopy photosynthesis of rice in Florida showed an average 54% stimulation in elevated CO₂ (Allen *et al.*, 1989).

Nijs *et al.* (1988) measured the rate of net CO₂ assimilation in perennial ryegrass (*Lolium perenne* L., cv *Vigor*) swards grown out of doors in small plastic chambers. In the elevated CO₂ treatment, canopy photosynthesis per unit ground area increased by 77% and dry matter production 43%.

The results of the Arctic tundra study showed that elevated CO₂ 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 CO₂ (Tissue & Oechel, 1987). The explanation appears to be due to at least two factors: first, *Eriophorum* showed considerable tillering in elevated CO₂, 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 CO₂. 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 CO₂'.

Temperature differences of 5°C or less appear to have little effect on the stimulation of photosynthesis by elevated CO₂. In a study of the temperature interaction with elevated CO₂ in rice, Allen *et al.* (1989) used three different temperature regimes, 28–21°C, 34–27°C and 40–33°C. Although the highest absolute values for canopy photosynthesis occurred in elevated CO₂ at the two lower temperature treatments, elevated CO₂ had the greatest relative effect on canopy photosynthesis at the highest growth temperatures (40–33°C). Similarly, the initial slope of the light response curve increased in elevated CO₂ compared to normal ambient CO₂ and the greatest relative increase occurred at the highest temperature. In soybean, a 5°C temperature difference (28–33°C) produced no measurable difference in canopy photosynthesis at either 330 cm³ m⁻³ or 800 cm³ m⁻³. The light response curves for both temperature treatments during full day measurements were identical (Jones *et al.*, 1985a) possibly because the temperature difference used in this study was close to optimum for both elevated and normal ambient CO₂.

Not surprisingly, the response of carbon assimilation to elevated CO₂ varies with the stage of development of the crop. Ackerson *et al.* (1984) showed that maintaining elevated CO₂ treatment throughout the life cycle of soybean increased yield. When CO₂ was applied only during the period from emergence to anthesis or only from anthesis through early pod development, the effect on yield was small. This suggests that elevated CO₂ promoted increased numbers of reproductive units, and that the carbon needed to satisfy the demand of pod fill was met from new photosynthate produced during the high CO₂ exposure rather than from stored carbohydrates.

Photosynthesis in plants grown in elevated CO₂ is often reported to be reduced after a period of exposure of some days' or weeks' duration (Cure & Acock, 1986; Delucia *et al.*, 1985; Percy & Bjorkman, 1983). This response has been called acclimation to acknowledge the fact that there have been adjustments in carbon metabolism. In a study of the tussock tundra dominated by *E. vaginatum*, Tissue & Oechel (1987) reported photosynthetic capacity completely acclimated to elevated CO₂ treatment within 3 weeks, after which plants grown at 660 cm³ m⁻³ had the same rate of photosynthesis as those grown and tested at 330 cm³ m⁻³. But not all studies of plants acclimating to elevated CO₂ have shown reduced capacity for photosynthesis. Some studies have reported either an increase or no change in photosynthetic capacity of elevated CO₂ (Arp & Drake, 1991; Conroy, 1989; Du Cloux *et al.*, 1989; Hollinger, 1987; Radin *et al.*, 1987; Valle *et al.*, 1985; Ziska *et al.*, 1991). See also the paper by W. Arp in this issue (pp. 869–875) regarding the regulation of the response to CO₂ by interaction between the source and sink.

Comparisons of canopy photosynthesis at both 330 and 800 cm³ m⁻³ for soybean canopies grown and tested in the different treatments showed that the CO₂ concentration during exposure accounted for 80% of the effect

of high CO₂ while acclimation during growth accounted for only 10% of the difference between treatment. Measurements of single leaf photosynthesis within the canopy of each treatment showed that there was no down regulation of photosynthesis (Valle *et al.*, 1985). Radin *et al.* (1987) showed that growth of the canopy in elevated CO₂ caused no apparent adjustment of photosynthetic capacity of cotton throughout the reproductive and boll fill stages.

The available data on the effects of elevated CO₂ on canopy photosynthesis suggest the following: (1) canopy photosynthesis increases in elevated CO₂ when there is a sink available for the carbon; (2) the relative effect of CO₂ is greatest at highest temperatures; and (3) elevated CO₂ alters many interacting factors, such as canopy architecture and partitioning of photoassimilates, that mediate gas exchange of canopies and ecosystems.

We will consider next the seasonal response of canopy photosynthesis in two salt marsh communities which differ from crops because they are perennial with large carbon storage capacities and they differ from each other in that one is a stand of a C₃ sedge and the other is a stand of a C₄ grass.

Canopy photosynthesis in a mesohaline salt marsh

Study site and chambers

The most intensive and longest running study of canopy photosynthesis has been taking place on a mesohaline salt marsh on the Chesapeake Bay, Maryland, U.S.A. Special attention is given to this study here because the data on canopy photosynthesis have not been previously reported. The study began in 1987 and the same sites have been exposed to the CO₂ treatment throughout the past four growing seasons. Two monospecific stands, one dominated by the C₃ sedge, *Scirpus olneyi*, and the other by the C₄ grass, *Spartina patens*, were exposed to twice-normal ambient CO₂ concentration throughout the four growing seasons of 1987–1990. Descriptions of the study site, construction details and microclimate of the open top chambers, measurements of above- and below-ground biomass production, nitrogen content and photosynthesis of single leaves in this study have been reported elsewhere (Arp & Drake, 1991; Curtis *et al.*, 1990; Curtis *et al.*, 1989a; Curtis, Drake & Whigham, 1989b; Drake *et al.*, in press; Long & Drake, 1991; Ziska, Drake & Chamberlain, 1990). Here, we report results of net ecosystem CO₂ exchange measurements (NCE_a, per unit area; NCE_b, per unit green biomass) determined periodically throughout the 1988 growing season within the chambers in which the test atmospheres were created.

NCE_a integrates the effects of elevated CO₂ on all aspects of ecosystem carbon metabolism including microbial respiration in the soil and decaying plant matter, root and shoot respiration, above ground biomass and canopy architecture, the timing of developmental processes, light and CO₂ distribution within the

canopy and photosynthetic properties of individual shoots. It also provides data by which models of ecosystem carbon balance can be tested.

The study site is located on a mesohaline marsh on a subestuary of the Chesapeake Bay where the C₃ sedge, *Scirpus olneyi*, and the C₄ grass, *Spartina patens*, form monospecific stands. These stands are an ideal outdoor laboratory for the study of elevated CO₂ because they provide the opportunity to compare the effects of CO₂ on ecosystem level processes determined by plants which differ in their fundamental capacity to respond to elevated CO₂ but which have evolved the anatomical and physiological mechanisms to cope with a common environment.

Open top chambers (0.8 m diameter by 1.0–1.5 m tall) constructed of aluminium tubing covered with a polyester film (Melinex 071, ICI, Delaware, U.S.A.) were established in five blocks of three units each in the two communities. Each block consisted of two sites with chambers and one without (control site). In five of the chambers in each community, air was enriched day and night with pure CO₂ to raise the concentration 340 cm³ m⁻³ above normal ambient. The other five chambers received normal ambient air. Details of the chamber design and microenvironment within them are discussed in Drake *et al.* (1989). Chambers were placed on the marsh in April at the first appearance of green shoots and kept there until no photosynthetic activity could be measured, which usually occurred by the 15 November.

Monitoring CO₂ concentration and net CO₂ exchange

Chamber air was continuously pumped to a gas manifold which fed an infrared gas analyser (BINOS, Model 092, Leybold-Heraeus, Hanau, Germany). See Leadley & Drake (in press) for a more detailed discussion of the modification of the open-top chamber for measurement of canopy photosynthesis. The CO₂ concentration of air within the chambers was measured approximately six times per hour. Approximately 35 s were required to flush the circuit, the dew point detectors and the analyser. The IRGA was automatically calibrated twice daily: once at sunrise and again at dusk. Air temperature within the canopy inside and outside the chambers was monitored with 25-gauge copper-constantin thermocouples. Temperature within the open top chambers averaged 2°C above the temperature in the canopy outside the chambers' Drake *et al.* (1989). At a central location, a pair of Eppley radiometers, fitted with appropriate cut-off filters, monitored incident photosynthetically active photon flux (PPF; 415–700 nm). Data were recorded using a Hewlett-Packard 3852 data acquisition system.

In order to measure ecosystem CO₂ exchange, an acrylic plastic top (3 mm thickness) with a chimney 20 cm in diameter and 50 cm high was added to the chamber. Addition of the top increased temperature inside the chamber by 1°C so that the temperature of the canopy in the chamber was an average of 3°C above the temperature of the canopy of the control site (no

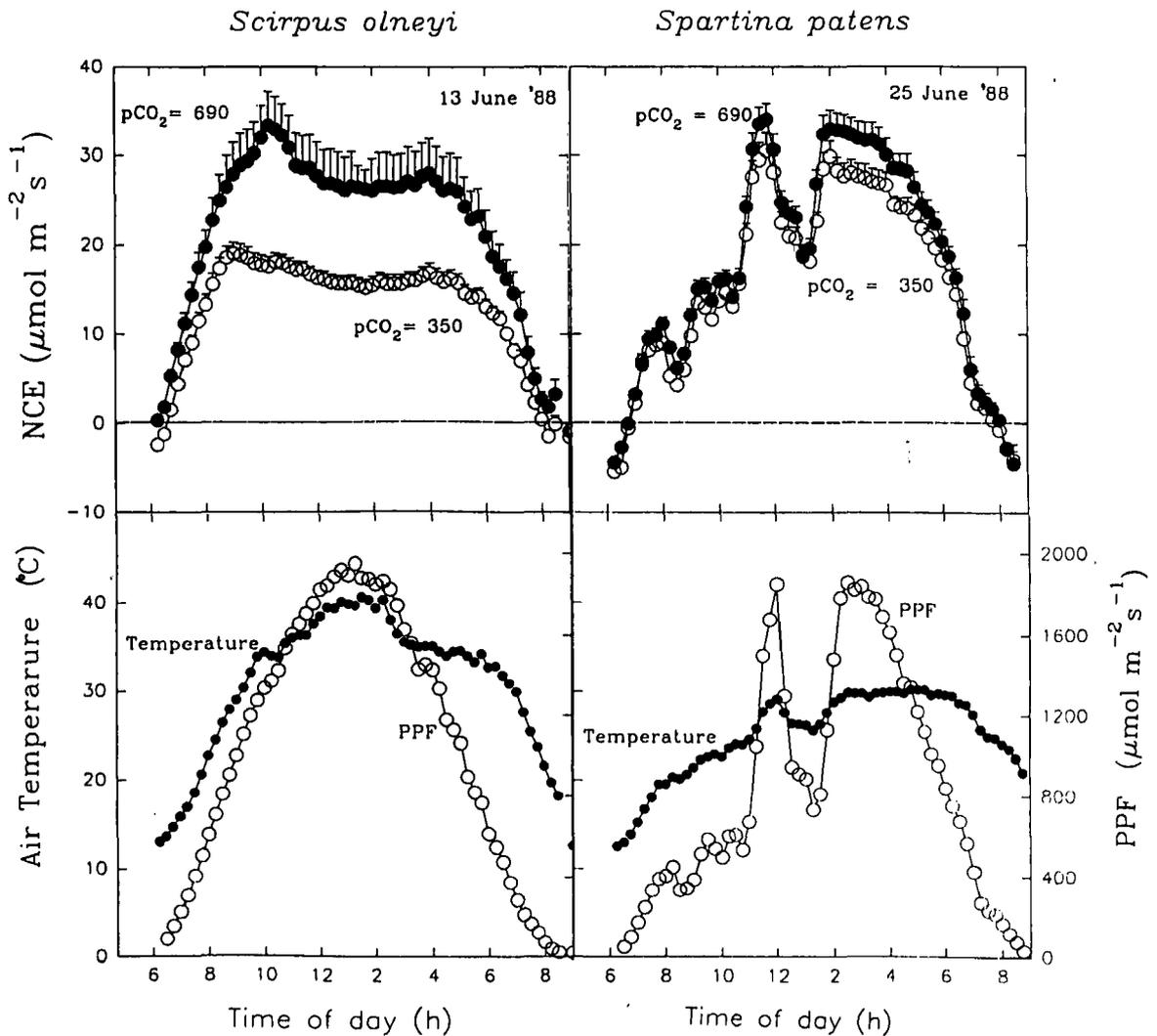


Figure 1. Net ecosystem CO_2 exchange per unit ground area (NCE_a) in the monospecific C_3 sedge, *Scirpus olneyi*, and in the C_4 grass, *Spartina patens*. Values are means and standard errors for five chambers in each community determined for 15-min intervals throughout the day. Throughout the paper, 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 .

chamber). NCE_a was determined from the difference between the CO_2 concentration of air entering and exiting the chamber, multiplied by the flow rate of air. Air flow through a pipe (10 cm ID) between the blower and chamber was determined periodically with a hot wire anemometer. Addition of the top with the chimney did not reduce the flow of air through the chamber.

Tops could be added and the system switched from open-top growth chambers to open gas exchange chambers for measuring NCE_a in one of the three communities in approximately an hour. The integrity of the gas circuit between the chambers in the field and the analyser was checked before measuring NCE_a by attaching both sampling lines to the same sampling port and allowing the zero voltage to be monitored for several h. This procedure helped to identify leaks, erratic pump performance or other problems which would com-

promise measurement of the CO_2 concentration difference.

Results

NCE_a of the *Scirpus olneyi* and *Spartina patens* communities is illustrated for two d in June 1988 (Fig. 1). Light response curves (Fig. 2) were constructed from the data in Fig. 1. NCE_a was averaged for all five chambers in each treatment in 15-min intervals throughout the day. The effect of elevated CO_2 is clearly evident in the C_3 community but much less in the C_4 -dominated community. NCE_a in the C_3 community saturated at a PPF near $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Light saturation did not occur and the light compensation value was higher in the C_4 than the C_3 community. Analysis of data for 10 d throughout the season for each community showed that

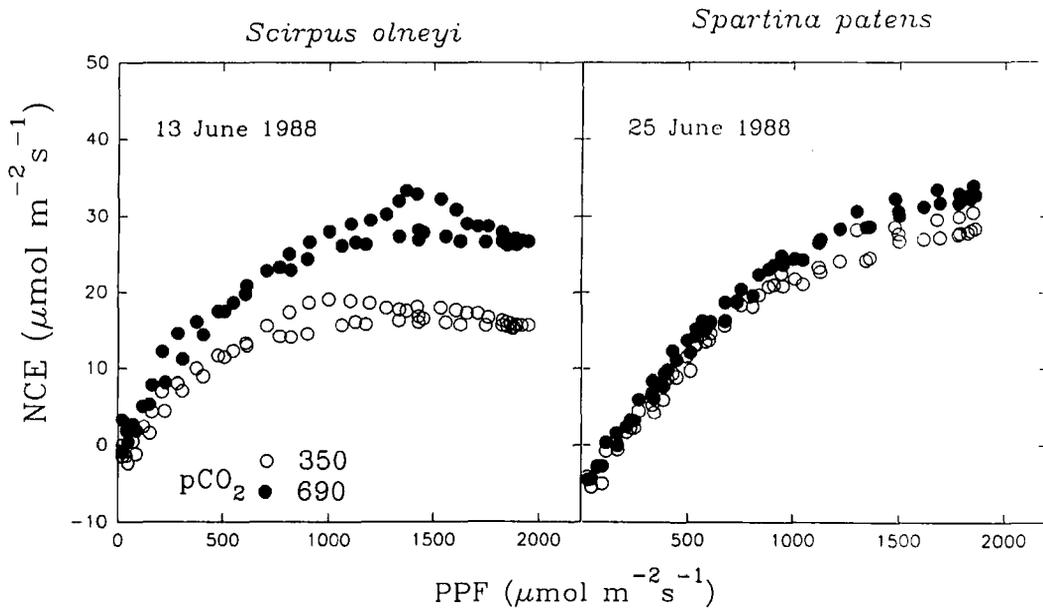


Figure 2. Light response curves created from the data values in Fig. 1 for the two communities.

the initial slope of the light response curve increased from May through August and declined thereafter. There were no significant differences between the initial slopes for the two treatments in either community primarily because of large day-to-day variations in the values. As shown in Fig. 1, $NCE_{m,x}$ values at midday for elevated and normal CO_2 treatments respectively were 25 and $17 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the *Scirpus olneyi* community, and 32 and $27 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the *Spartina patens* community. This represents a CO_2 stimulation of 49% in the *Scirpus olneyi* community and 19% in the *Spartina patens* community.

NCE_a for the C_3 *Scirpus olneyi* and the C_4 *Spartina patens* communities for 1988 are presented in Fig. 3. Total carbon assimilated throughout the daytime hours was determined from the integration of the seasonal trends (Fig. 3) and are shown in Table 1 in terms of dry weight equivalents. Elevated CO_2 increased carbon accumulation by 88% in the *Scirpus olneyi* community and 40% in the *Spartina patens* community.

The relative effect of elevated CO_2 on biomass production and NCE_a was time dependent (Fig. 4). The stimulation of both NCE_a and biomass production increased with time. However, there was very little

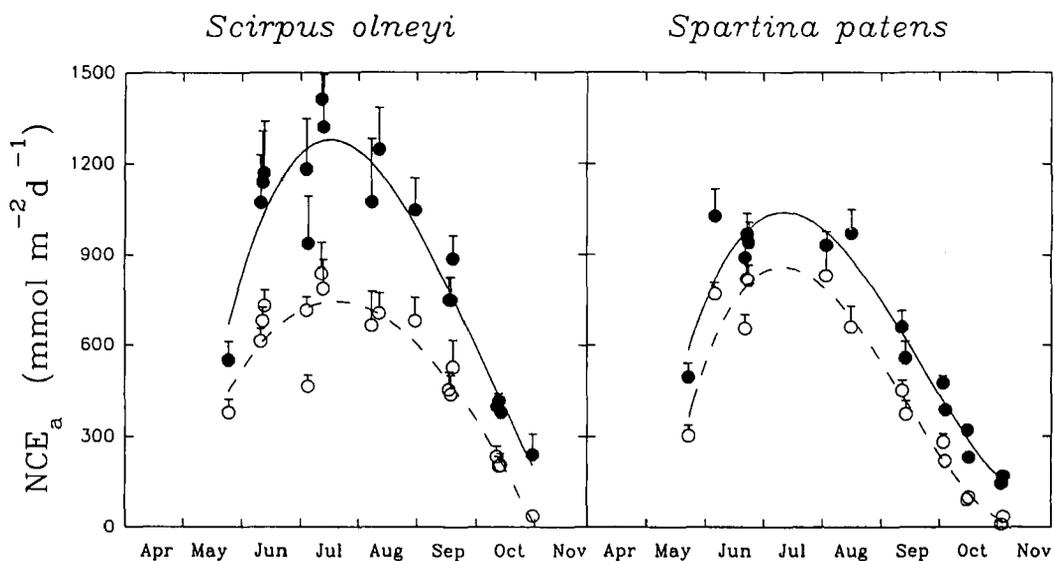


Figure 3. Daily NCE_a for five chambers in each community at each CO_2 treatment. The lines are third-order polynomial regressions. In both communities, the data sets are significantly different at the 0.05 level of significance in a paired t -test. Each value is the mean and standard error bar of whole day integrations of NCE when PPF was greater than $50 \mu\text{mol m}^{-2} \text{s}^{-1}$.

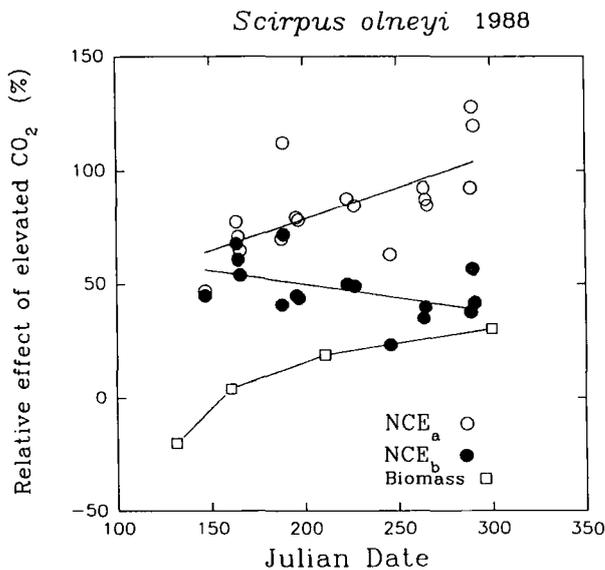


Figure 4. The relative effect of elevated CO₂ on biomass production, NCE_a and NCE_b.

effect on NCE_b (=NCE_a divided by biomass per m²), which declined slightly throughout the season. The seasonal average effect of elevated CO₂ on NCE_b was a 48% increase.

Discussion

Long-term exposure to elevated CO₂ increased carbon accumulation in the ecosystem 88% in the C₃ and 40% in the C₄ plant community (Table 1). These results of measurements of canopy photosynthesis are consistent with measurements of photosynthesis in single attached leaves from this study. Ziska *et al.* (1990) reported that in 1988 light saturated photosynthesis in whole attached stems of *Scirpus olneyi* was increased by 60–73% in elevated CO₂ compared to normal ambient CO₂, and similarly, by 26–38% in those of *Spartina patens*. Turitzin & Drake (1981) concluded that the planophile architecture of this C₄ grass community limits diffusion

Table 1. Integrated net dry weight accumulation for two plant communities for the 1988 growing season (kg m⁻²). Third-order polynomial regressions of the dependence of integrated NCE per day for both treatments in each community were fitted to the data values in Fig. 3. Total carbon accumulated was determined by summing the daily values predicted by the regression for the period 1 May through 15 November. Dry weight equivalents were computed by assuming an average 44% carbon in the plant tissue (Curtis *et al.*, 1989b). The relative effect of elevated CO₂ on ecosystem carbon assimilation is given by the third column

Community	Carbon accumulation (kg m ⁻²)		Increase (%)
	Elevated CO ₂	Ambient CO ₂	
<i>Scirpus olneyi</i> (C ₃)	2.48	1.32	88
<i>Spartina patens</i> (C ₄)	1.80	1.29	40

of CO₂ and results in CO₂ starvation. This effect may have been intensified by water stress which would close stomata, reducing intercellular CO₂ even further, and cause reduction of canopy photosynthesis. In 1988, a very hot, dry year, plant water potential declined to -3.5MPa during midday (Arp *et al.*, 1991). In this event, elevated CO₂ would overcome CO₂ depletion within the plant and within the canopy. In this study, elevated CO₂ increased plant water potential by approximately 0.5MPa above that of plants grown in normal ambient CO₂ (Arp *et al.*, 1991). These combined effects may have contributed to the large effect of elevated CO₂ on NCE_a in both communities but especially in the C₄ community.

Several mechanisms affecting ecosystem gas exchange contributed to the high seasonal carbon accumulation in the C₃ community. First, photosynthetic capacity of green shoots increased (Arp & Drake, 1991; Ziska *et al.*, 1990). Second, quantum yield was higher in elevated CO₂ (Long & Drake, 1991). This would reduce the light compensation point, extend the period of positive carbon accumulation throughout the day and increase the rate of photosynthesis within the plant canopy. Third, elevated CO₂ increased the number of green shoots and this effect increased throughout the season (Fig. 4; Curtis *et al.*, 1989a). Fourth, the rate of senescence of these additional shoots was reduced in elevated CO₂ which effectively extended the growing season for canopy NCE_a (Curtis *et al.*, 1989a). Finally, elevated CO₂ increased water potential in both the C₃ and C₄ plant communities (Arp *et al.*, 1991). Other factors influenced indirectly by the increased availability of carbon must contribute to the ecosystem response to rising CO₂. These factors include altered canopy structure, increased soil carbon and respiration.

There is no evidence in the data reported here for either *Scirpus olneyi* or *Spartina patens* that growth in elevated CO₂ results in down regulation of photosynthesis. Data on quantum yield and photosynthetic capacity of *Scirpus olneyi*, measured in plants after 3 and 4 years of growth, respectively, provide no evidence that down regulation of metabolic aspects of photosynthesis occurred (Arp & Drake, 1991; Long & Drake, 1991). In fact, data obtained in August and September 1990 indicated that photosynthetic capacity is increased after acclimation to high CO₂ (Arp & Drake, 1991).

Arp (1991, this issue, pp. 869–875) points out that, in many of the acclimation responses reported to date, the effect of elevated CO₂ on photosynthetic capacity is inversely correlated with rooting volume during the CO₂ treatment. Photosynthetic capacity of plants exposed to elevated CO₂ while growing in small pots (<10 dm³) was less than in plants grown in normal ambient CO₂, while photosynthetic capacity of plants grown in large pots or in the field was the same or greater than in plants grown in normal ambient CO₂.

The studies of canopy photosynthesis reviewed in this paper indicate that elevated atmospheric CO₂ increases CO₂ assimilation by 25–50%. This appears to be slightly higher than anticipated from laboratory studies. There is

no evidence in this data set to support the notion that the effects of rising CO₂ would not be sustained.

Acknowledgments

We wish to thank Caton Gauthier for assistance in the preparation of the manuscript and Willem Arp, Craig Cohen, Carol Greitner, Grace Ju, Gary Peresta and Perry Rapp for helpful comments on the manuscript. This work was supported by a grant to the Smithsonian Institution from the U.S. Department of Energy and by additional supporting funds from the Smithsonian Institution.

References

- Ackerson, R.C., Havelka, U.D. & Boyle, M.G. (1984) CO₂-enrichment effects on soybean physiology. II. Effects of stage-specific CO₂ exposure. *Crop Science*, **24**, 1150–1154.
- Acock, B. & Allen, L.H., Jr (1985) Crop responses to elevated carbon dioxide concentrations. In *Direct Effects of Increasing Carbon Dioxide on Vegetation* (eds B.R. Strain & J.D. Cure), pp. 53–97. United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division, Washington, D.C.
- Acock, B., Reddy, V.R., Hodges, H.F., Baker, D.N. & McKinion, J.M. (1985) Photosynthetic response of soybean canopies to full-season carbon dioxide enrichment. *Agronomy Journal*, **77**, 942–947.
- Allen, L.H., Jr, Boote, K.J., Jones, P.H., Jones, J.W., Rowland-Bamford, A.J., Bowes, G., Baker, J.T. & Laugel, F. (1989) *Temperature and CO₂ effects on rice 1988*. United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division, Washington, D.C.
- Arp, W.J. (1991) Effects of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant, Cell and Environment*, **14**, 869–875.
- Arp, W.J. & Drake, B.G. (1991) Increased photosynthetic capacity of *Scirpus olneyi* after 4 years of exposure to elevated CO₂. *Plant, Cell and Environment*, **14**, 1004–1008.
- Arp, W.J., Drake, B.G., Pockman, W.T., Curtis, P.S. & Whigham, D.F. (1991) Effects of four years exposure to elevated atmospheric CO₂ on competition between C₃ and C₄ salt marsh species. *Vegetatio*, in press.
- Conroy, J. (1989) *Influence of high CO₂ on Pinus radiata*. Ph.D. Thesis, Macquarie University, School of Biological Sciences, Canberra, Australia.
- Cure, J.D. (1985) Carbon dioxide doubling responses: a crop survey. In *Direct Effects of Increasing Carbon Dioxide on Vegetation* (eds B.R. Strain & J.D. Cure), pp. 99–116. United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division, Washington, D.C.
- Cure, J.D. & Acock, B. (1986) Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology*, **38**, 127–145.
- Curtis, P.S., Balduman, L.M., Drake, B.G. & Whigham, D.F. (1990) Elevated atmospheric CO₂ effects on belowground processes in C₃ and C₄ estuarine marsh communities. *Ecology*, **71**, 2001–2006.
- Curtis, P.S., Drake, B.G., Leadley, P.W., Arp, W.J. & Whigham, D.F. (1989a) Growth and senescence in plant communities exposed to elevated CO₂ concentrations on an estuarine marsh. *Oecologia*, **78**, 20–26.
- Curtis, P.S., Drake, B.G. & Whigham, D.F. (1989b) Nitrogen and carbon dynamics in C₃ and C₄ estuarine marsh plants grown under elevated CO₂ *in situ*. *Oecologia*, **78**, 297–301.
- Delucia, E.H., Sasek, T.W. & Strain, B.R. (1985) Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosynthesis Research*, **7**, 175–184.
- Drake, B.G., Arp, W.J., Long, S.P. & Lawlor, D.W. (in press) Photosynthesis of the C₃ sedge, *Scirpus olneyi*, after long-term exposure to elevated CO₂ in open top chambers in the field. In *Trends in Photosynthesis Research* (eds J.B. Barber, H. Medrano & M.G. Guerrero). Intercept Ltd, Andover.
- Drake, B.G., Leadley, P.W., Arp, W.J., Nassiry, D. & Curtis, P.S. (1989) An open top chamber for field studies of elevated atmospheric CO₂ concentration on saltmarsh vegetation. *Functional Ecology*, **3**, 363–371.
- Du Cloux, H., Andre, M., Gerbaud, A. & Daguene, A. (1989) Wheat response to CO₂ enrichment: effect on photosynthetic and photorepiratory characteristics. *Photosynthetica*, **23**, 145–153.
- Goudriaan, J. & Ajtay, G.L. (1979) The possible effects of increased CO₂ on photosynthesis. In *The Global Carbon Cycle* (eds B. Bolin, E.T. Degens, S. Kempe & P. Ketner), pp. 237–249. John Wiley & Sons, Chichester.
- Gulke, N.E., Riechers, G.H., Oechel, W.C., Hjelm, U. & Jaeger, C. (1990) Carbon balance in tussock tundra under ambient and elevated atmospheric CO₂. *Oecologia*, **83**, 485–494.
- Havelka, U.D., Ackerson, R.C., Boyle, M.G. & Wittenback, V.A. (1984) CO₂-enrichment effects on soybean physiology. I. Effects of long-term CO₂ exposure. *Crop Science*, **24**, 1146–1150.
- Hollinger, D.Y. (1987) Gas exchange and dry matter allocation responses to elevation of atmospheric CO₂ concentration in seedlings of three tree species. *Tree Physiology*, **3**, 193–202.
- Jarvis, P.G. (1989) Atmospheric carbon dioxide and forests. *Philosophical Transactions of the Royal Society of London B*, **324**, 369–392.
- Jones, P., Allen, L.H., Jr & Jones, J.W. (1985a) Responses of soybean canopy photosynthesis and transpiration to whole-day temperature changes in different CO₂ environments. *Agronomy Journal*, **77**, 242–249.
- Jones, P., Allen, L.H., Jr, Jones, J.W. & Valle, R. (1985b) Photosynthesis and transpiration responses of soybean canopies to short- and long-term CO₂ treatments. *Agronomy Journal*, **77**, 119–126.
- Jones, P., Allen, L.H., Jr, Jones, J.W., Boote, K.J. & Campbell, W.J. (1984) Soybean canopy growth, photosynthesis, and transpiration responses to whole-season carbon dioxide enrichment. *Agronomy Journal*, **76**, 633–637.
- Jordan, D.B. & Ogren, W.L. (1984) The CO₂/O₂ specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulose-bisphosphate concentration, pH and temperature. *Planta*, **161**, 308–313.
- Kimball, B.A. (1983) Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal*, **75**, 779–788.
- Kramer, P.J. (1981) Carbon dioxide concentration, photosynthesis, and dry matter production. *BioScience*, **31**, 29–33.
- Leadley, P.W. & Drake, B.G. (in press) Open top chambers for exposing a grassland community to elevated CO₂ concentration and for measuring net ecosystem gas exchange. *Vegetatio*.
- Long, S.P. & Drake, B.G. (1991) Effect of the long-term elevation of CO₂ concentration in the field on the quantum yield of photosynthesis of the C₃ sedge, *Scirpus olneyi*. *Plant Physiology*, **96**, 221–226.
- Mauney, J.R., Guinn, G., Fry, K.E. & Hesketh, J.D. (1979) Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sunflower and sorghum. *Photosynthetica*, **13**, 260–266.
- Nijs, I., Impens, I. & Behaeghe, T. (1988) Effects of rising atmospheric carbon dioxide concentration on gas exchange and growth of perennial ryegrass. *Photosynthetica*, **22**, 44–50.
- Oechel, W.C. & 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 & J.D. Cure), pp. 117–154. United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Division, Washington, D.C.
- Overdieck, D. & Lieth, H. (1986) *Final report of the project: long-term effects of increased atmospheric CO₂ concentration level on terrestrial plants in model-ecosystems*. Universität Osnabrück, Fachbereich Biologie/Chemie, Arbeitsgruppe Ökologie. Osnabrück.
- Pearcy, R.W. & Bjorkman, O. (1983) Physiological effects. In *CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide* (ed. E.R. Lemon), pp. 65–105. Westview Press, Boulder, CO.
- Radin, J.W., Kimball, B.A., Hendrix, D.L. & Mauney, J.R. (1987)

- Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field. *Photosynthesis Research*, **12**, 191–203.
- Sionit, N., Rogers, H.H., Bingham, G.E. & Strain, B.R. (1984) Photosynthesis and stomatal conductance with CO₂-enrichment of container- and field-grown soybeans. *Agronomy Journal*, **76**, 447–451.
- Tissue, D.T. & Oechel, W.C. (1987) Response of *Eriophorum vaginatum* to elevated CO₂ and temperature in the Alaskan tussock tundra. *Ecology*, **68**, 401–410.
- Turitzin, S.N. & Drake, B.G. (1981) The effect of a seasonal change in canopy structure on the photosynthetic efficiency of a salt marsh. *Oecologia*, **48**, 79–84.
- Valle, R., Mishoe, J.W., Campbell, W.J., Jones, J.W. & Allen, L.H. Jr (1985) Photosynthetic responses of 'Bragg' soybean leaves adapted to different CO₂ environments. *Crop Science*, **25**, 333–339.
- Ziska, L.H., Drake, B.G. & Chamberlain, S. (1990) Long-term photosynthetic response in single leaves of a C₃ and C₄ salt marsh species grown at elevated atmospheric CO₂ *in situ*. *Oecologia*, **83**, 469–472.
- Ziska, L.H., Hogan, K.P., Smith, A.P. & Drake, B.G. (1991) Growth and photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. *Oecologia*, **86**, 383–389.