

An open top chamber for field studies of elevated atmospheric CO₂ concentration on saltmarsh vegetation

B. G. DRAKE, P. W. LEADLEY,
W. J. ARP, D. NASSIRY and
P. S. CURTIS

*Smithsonian Environmental Research Center,
Box 28, Edgewater, Maryland 21037, USA*

Abstract. Small open top chambers (0.8 m × 1.0 m) were developed to maintain elevated CO₂ concentrations in three plant communities in a brackish marsh ecosystem. Mean annual CO₂ concentrations were 350 ± 22 μl l⁻¹ in chambers which received no added CO₂ and 686 ± 30 μl l⁻¹ in chambers with elevated CO₂ concentrations. Light quality was not affected in the photosynthetically active wavelengths but the chamber reduced light quantity by 10%. Night-time air temperatures inside the chamber (T_i) averaged 2°C above air temperature outside the chamber (T_o) due to heating from the air blowers. Air temperature profiles through the plant canopy and boundary layer showed that daytime temperature differences ($T_i - T_o$) were greater than night-time differences and this day/night difference also depended on the plant community. Effects of the chamber on the micro-environment of the plant communities resulted in a significant growth enhancement in the plant community dominated by the C₃ sedge *Scirpus olneyi* Grey but not in the other two communities.

Key-words: Elevated CO₂, open top chamber, microclimate

Introduction

The rise in atmospheric carbon dioxide concentration has led to efforts to determine the effect of this change on vegetation (Acock & Allen, 1985; Kimball, 1983; Bazzaz, Garbutt & Williams, 1985). The wide range of responses among species to elevated CO₂ and the effects of environmental variables on these responses make it difficult to construct general models of plant response to rising CO₂ concentration. Ecosystem level responses that might occur, such as changes in species composition and carbon sequestering, remain highly

speculative. Long term exposure of plants in the field to elevated CO₂ is necessary to improve our understanding of the ecological effects of this change in atmospheric composition.

Many different approaches have been used to generate elevated CO₂ atmospheres including leaf chambers, controlled environment chambers (i.e. phytotrons, portable growth chambers, sunlit controlled environment chambers), greenhouses, field environment tracking chambers and open top chambers (Drake, Rogers & Allen, 1985). Most of these have been used in studies of crop species (Acock & Allen, 1985) but wild plants and ecosystem processes have received much less attention (Bazzaz *et al.*, 1985; Overdieck, Bossemeyers & Leith, 1984; Hilbert, Prudhomme & Oechel, 1987; Oechel & Strain, 1985).

Drake *et al.* (1985) concluded that the open top chamber offers the best compromise between the need for controlling temperature in closed environments such as those used by Jones *et al.* (1984) and Prudhomme *et al.* (1984) and the high cost and complex technical demands of the unrestricted release of CO₂. Open top chambers were first used for field studies of the effects of air pollution and were later adapted for elevated CO₂ research (Heagle, Body & Heck, 1973; Heagle *et al.*, 1979; Rogers *et al.*, 1983). This paper describes a modification of the open top chamber design for use in field studies of the effects of increased CO₂ concentration on unmanaged wetlands vegetation. We give details of the control of CO₂ concentration and the effect of the chamber on micro-environment and plant growth. In a subsequent paper we will describe the use of the chamber for measuring net ecosystem exchange of water vapour and CO₂.

Materials and methods

Site description

This study was conducted on a brackish marsh located on the Rhode River, a sub-estuary of the Chesapeake Bay. Three plant communities were studied: one dominated by *Scirpus olneyi* Grey; one by *Spartina patens* (Ait.) Muhl.; and the third by a mixture of *S. olneyi*, *S. patens* and *Distichlis*

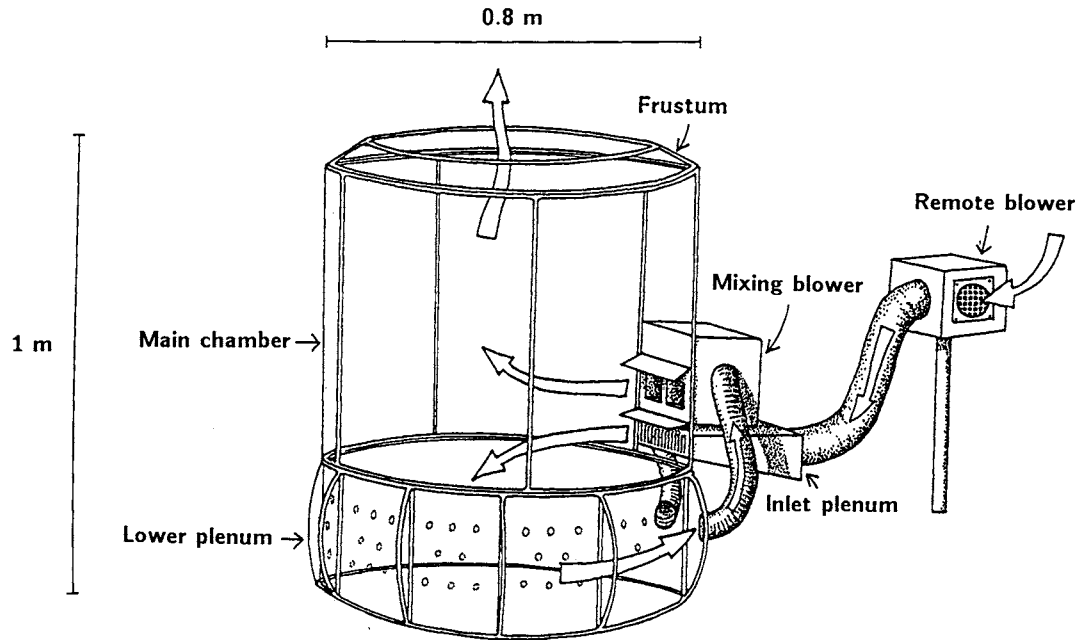


Fig. 1. Open top chamber detailing flow of air. Air is drawn into the remote blower and blown through the inlet plenum into the chamber. The mixing blower draws air from inside the chamber through the perforated inner wall of the lower plenum and blows it back into the chamber. Air exits the chamber through the frustum.

spicata (L.) Greene. These will be referred to as the Scirpus, Spartina and mixed communities respectively.

Chamber construction and operation

Plant species in the marsh ecosystem were relatively short (<1.2 m in height) and grew in dense stands (c 400–4000 shoots m^{-2}), which allowed smaller chambers than those in use for crop species. Irregular flood tides required that the chamber be easily dismantled and removed. A frustum was included in the design because it had been shown to significantly reduce incursion of air into open top chambers during windy conditions (Davis & Rogers, 1980; Unsworth, Heagle & Heck, 1984).

The chamber components are shown in Fig. 1. Overall dimensions were 0.8 m diameter and 1.0 m height. The chamber framework of welded aluminium tubing (0.85 cm inside diameter (ID), 0.2 cm wall thickness) was painted with white polyurethane. Chambers were built in three sections: a lower plenum, main chamber and frustum. A 53 cm tall extension to the main chamber made with a PVC frame was added in the Scirpus community when the vegetation height exceeded c 0.9 m. Clear polyester film (Melinex 071, ICI, Delaware, USA) was attached to the framework with polyester tape. Air was introduced and mixed

in the chambers by two squirrel-cage blowers. The remote blower (4C015B, Dayton Electric Manufacturer, Illinois, USA) was mounted separate from the chamber and the mixing blower (4C443A, Dayton Electric Manufacturer, Illinois, USA) was mounted in an aluminium box welded to the chamber frame. Insulated ducting (10.2 cm ID) connected the remote blower to the inlet plenum. Two sections of uninsulated ducting (7.5 cm ID) are used to connect the lower plenum to the mixing blower.

Air circulation within the chamber is illustrated in Fig. 1. A small amount of pure CO_2 was injected into the air stream at the remote blower to elevate the CO_2 concentration. Air from each chamber was continuously sampled by a pump located near the chamber in the field. The sample stream was delivered to the laboratory via a series of three mixing volumes of 3.8 l each. Water vapour was purged from the sample before injection into the gas analyser. CO_2 concentrations in these continuous air samples were measured automatically in each chamber every 15 min using an infra-red gas analyser (Binos 4B.2, Leybold-Heraeus, Hanau, Federal Republic of Germany) and data acquisition computer (HP 3852A, Hewlett Packard, California, USA). The gas analyser was calibrated with gas standards of CO_2 in air diluted by a known amount of CO_2 free air using a system of critical flow orifices. Seasonal mean CO_2 concen-

trations were determined from measurements made in the open top chambers from 23 April through 10 November 1987. The sampling point was in the centre of each chamber, just above the top of the canopy (*c* 40 cm above the marsh surface) in the *Spartina* and mixed communities and within the top of the canopy (*c* 70 cm above the marsh surface) in the *Scirpus* community (Fig. 3). Horizontal and vertical profiles of CO₂ concentration were measured inside a *Spartina* and a *Scirpus* chamber. Vertical profiles of CO₂ concentration outside the chambers were measured in the *Scirpus* community.

Light

The transmission spectrum of the chamber covering was measured with a Cary spectrophotometer. Light quantity inside and outside the chambers was monitored with quantum sensors (LI-190S, LI-COR Inc., Nebraska, USA) placed immediately above the canopy in the centre of the chamber. Light was measured every 30 s and 5 min averages were stored.

Air movement

Wind speed was measured within the chamber using a hot wire anemometer (1440M, Kurtz Institute Inc., California, USA) at five levels along two transects bisecting an empty chamber sealed at the bottom.

Temperature

Air temperature measurements were made with copper-constantan thermocouples 0.55 mm diameter shielded from downward radiation with aluminium foil. The contribution of the two blowers to chamber heating was determined by placing thermocouples before and after each blower. Vegetation temperatures were measured using a hand-held, infra-red thermometer (210, Everest Interscience, California, USA).

Vegetation measurement

Ten chambers were placed in the *Scirpus*, *Spartina* and mixed communities on 15 April 1987 and maintained there until 15 November 1987. Half of the chambers in each community received no additional CO₂ (ambient treatment) and half received enough CO₂ to raise the concentration *c* 340 $\mu\text{l l}^{-1}$ above the ambient concentration beginning 23 April 1987 (elevated treatment). Unchambered control sites were also monitored. Chambers

were sealed to the marsh by taping the bottoms to plastic garden edging inserted to a depth of 10 cm into the marsh substrate. Plant growth was followed by serial, non-destructive censuses of shoot number and height. Biomass was then determined from destructive subsamples in the mixed and *Spartina* communities or from allometric relationships between shoot height and biomass in the *Scirpus* community (see Curtis *et al.*, 1989 for a description of sampling methods).

Results and discussion

CO₂ concentration

The most important task of the open top chamber was to generate test atmospheres of elevated CO₂ concentration. Mean CO₂ (or pollutant) concentrations in open top chambers are typically reported for measurements made throughout the experiment taken from a single point. Data of this type provide information about the temporal variability of CO₂ concentration. Seasonal mean daytime CO₂ concentrations measured in the elevated treatment in each of the three communities are given in Table 1. Average CO₂ concentrations in elevated chambers were 333, 336 and 338 $\mu\text{l l}^{-1}$ above ambient concentration for the *Spartina*, mixed and *Scirpus* communities. The variability in CO₂ concentration increased during windy periods. For example, on a day with winds averaging 1.2 m s⁻¹, CO₂ concentrations in the elevated chambers were 336 \pm 16 (SD) $\mu\text{l l}^{-1}$ above ambient concentrations but on a day with winds averaging 4.3 m s⁻¹, CO₂ concentrations were 355 \pm 53 $\mu\text{l l}^{-1}$ above ambient concentrations.

Fig. 2 shows the spatial variability in elevated CO₂ concentration in an open top chamber from both the *Spartina* and *Scirpus* communities. CO₂ concentration in the *Spartina* chamber was highest

Table 1. Daytime (sunrise to sunset) mean CO₂ concentration in elevated and ambient chambers from the three marsh communities. Mean \pm SD (*n*).

	CO ₂ ($\mu\text{l l}^{-1}$)
Elevated	
<i>Spartina</i>	683 \pm 29 (844) ⁺
Mixed	686 \pm 31 (855)
<i>Scirpus</i>	688 \pm 31 (844)
Pooled	686 \pm 30 (2543)
Ambient	
Pooled	350 \pm 22 (169)

⁺ Each observation is the average CO₂ concentration on one day for a single chamber.

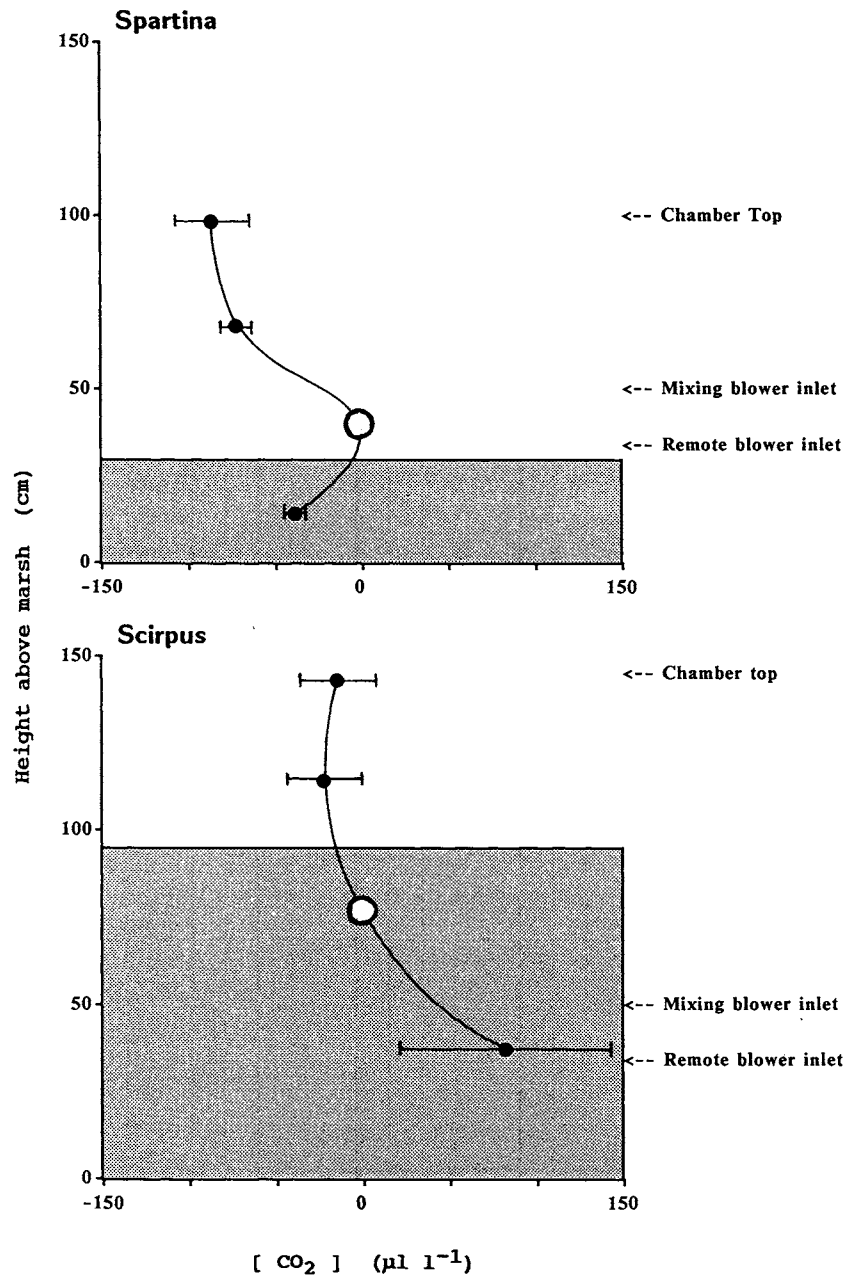


Fig. 2. Deviation of CO_2 concentrations (●) from the set point (○) along a height profile inside an open top chamber in the *Spartina* and *Scirpus* communities during the daytime. Error bars represent the deviation from the mean for four light periods in the *Spartina* and five light periods in the *Scirpus* community. Shading represents the height of the vegetation.

in front of the inlet plenum. CO_2 concentration in the *Scirpus* chamber at the inlet plenum height was $83 \pm 61 \mu\text{l l}^{-1}$ higher than at the normal sampling position near the top of the canopy. Spatial heterogeneity of CO_2 concentration in the *Spartina* chamber was similar to that reported for open top chambers with frustums (Davis & Rogers, 1980). Spatial heterogeneity in the *Scirpus* cham-

ber was similar to reported values for open top chambers without frustums (Heagle *et al.*, 1973, 1979; Davis & Rogers, 1980).

CO_2 concentration outside the chambers in the *Scirpus* community was nearly constant with height during midday, with average CO_2 concentrations below $350 \mu\text{l l}^{-1}$ and very slight depressions in CO_2 concentration in the middle of the

canopy (Fig. 3). On windy nights CO₂ concentration was more variable and higher than during midday by 50–100 $\mu\text{l l}^{-1}$. However, on still nights CO₂ concentration was highly variable and very much higher than during windy nights. For example, on one night it was 780 $\mu\text{l l}^{-1}$ near the bottom of the canopy and 500 $\mu\text{l l}^{-1}$ at 3 m (Fig. 3) and it has been recorded as high as 1200 $\mu\text{l l}^{-1}$. High night time CO₂ concentration was due to the accumulation of respiratory CO₂ evolving from the marsh sediments, marsh vegetation and the adjacent forest. The marsh was surrounded on three sides by forested uplands, forming a natural drainage basin for air flow from the forest canopy. Our data show that these marsh communities are exposed to a CO₂ concentration at night which is 100–700 $\mu\text{l l}^{-1}$ higher than CO₂ concentration during the day.

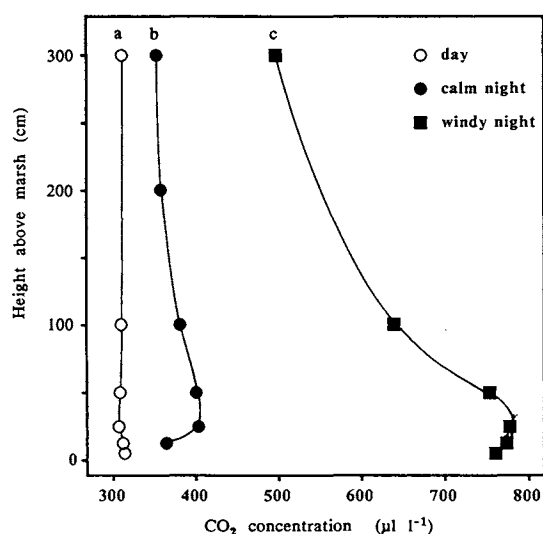


Fig. 3. CO₂ profiles above the marsh in the *Scirpus* community during the day (curve a), on a windy night (curve b) and calm night (curve c). CO₂ concentrations represent a single measurement at each height above the marsh. Measurement dates were 18 August (a, c) and 24 August (b), 1987.

Light

The UV stabilizers on both sides of the polyester covering blocked transmission in the UV region below 380 nm. Transmission in the photosynthetically active spectrum (400–700 nm) increased from 85% at 400 nm to 90% at 700 nm. The manufacturer's specifications indicated that about 25% of longwave radiation above 3000 nm was reflected and about 8% absorbed.

Fig. 4 shows a comparison between incident photosynthetically active photon flux (PPF, 400–700 nm) inside and outside an open top chamber

over a 24 h period. Transmission of PPF was approximately 90% (Fig. 4, inset). Other studies using arrays of quantum sensors have reported light attenuation in large open top chambers to be 10–15% and dependent on solar angle (Heagle *et al.*, 1979; Olszyk, Tibbitts & Hertzberg, 1980; Weinstock, Kender & Musselman, 1982).

Air movement

Wind speeds ranged from 1.6 m s⁻¹ directly in front of the blower to 0.1 m s⁻¹ along the side of the chamber opposite the inlet plenum (Fig. 5). Highest wind speed occurs in front of the inlet and mixing blowers. Average wind speed was *c* 0.4 m s⁻¹. The most obvious effect of the chamber on windspeed in the plant canopy was that it was constant while outside the chamber it was variable. The purpose of the mixing blower was to increase turbulence and heat exchange within the chamber. Average windspeeds in large open top chambers have been reported to be between 0.3 and 0.8 m s⁻¹ (Heagle *et al.*, 1979; Olszyk *et al.*, 1980; Weinstock *et al.*, 1982). There were larger variations in windspeed across this chamber because air was blown directly into the chamber rather than through a perforated plenum as in the large open top chambers. Another difference between this chamber design and the larger open top chambers was the air path which was directed over the top of or into the middle of the plant canopy and then downward around the sides.

Air temperature

Air temperature profiles were constructed from temperatures measured with shielded thermocouples located at several positions from near the surface to 2 m (Fig. 6). At night, air temperature outside the chamber (*T*_o) was lowest at about 40 cm in the mixed community, and between 30 and 80 cm in the *Scirpus* community (Fig. 6a and 6b, curve I). The shape of this profile is characteristic of an inversion condition (Rosenberg, 1974; Hiramatsu, Seo & Maitani, 1984). Air temperature inside the chambers (*T*_i) at night was 1–2 °C higher than *T*_o (Fig. 6a and 6b, curve II). Thermocouples placed before and after the remote and mixing blowers demonstrated that each blower raised air temperatures about 1.2 °C. Each blower required about 70 watts of power, which was sufficient to produce the observed heating.

During the day, temperature profiles outside the chambers (Fig. 6a and 6b, curve III) were typical of lapse conditions (Rosenberg, 1974; Hiramatsu *et*

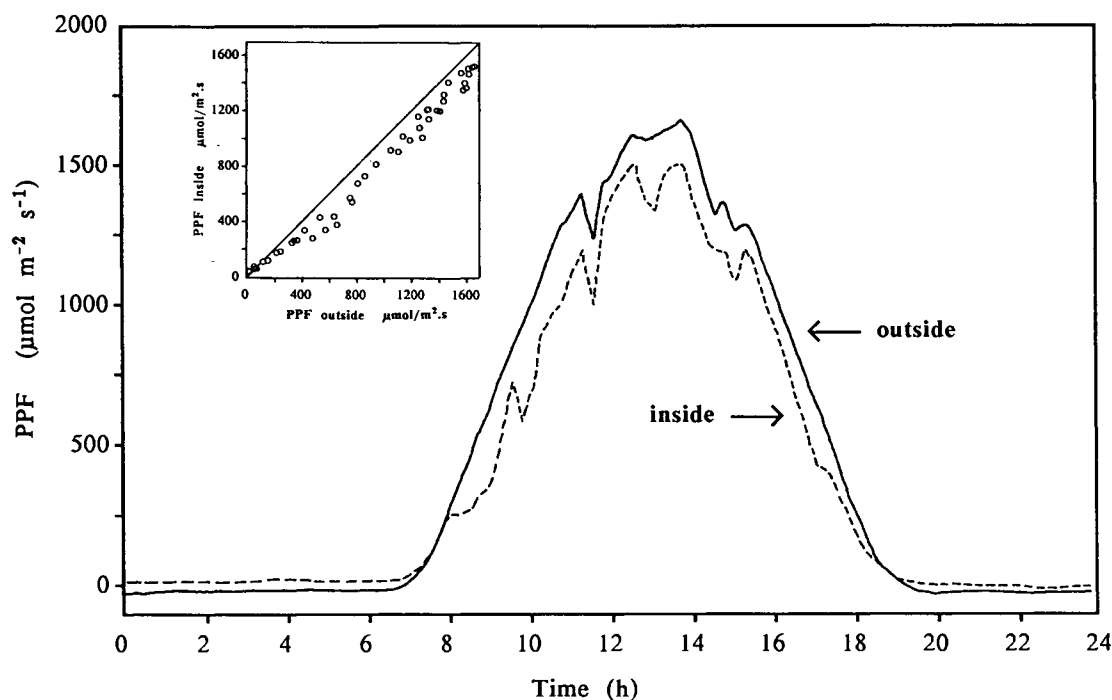


Fig. 4. 24-h record of PPF inside and outside an open top chamber. Inset, PPF inside as a function of PPF outside. Individual points represent 15 min averages of measurements taken every 30 s.

al., 1984). In the mixed community, T_o was lowest above the canopy and increased downward toward the marsh surface (Fig. 6a, curve III). Inside the chamber the temperature profile was distorted by introduction of cooler air drawn from above the canopy by the remote blower and by turbulence generated by the circulating blower (Fig. 6a, curve IV). Air was drawn into the chamber at 0.7 m, blown down over the plants at about 0.4 m, heated by the vegetation, drawn into the lower plenum, and reintroduced into the chamber at 0.5 m (compare curves III and IV, Fig. 6b). Temperature profiles in the *Scirpus* community were similar to those in the mixed community except that T_i was 2–4°C higher than T_o (Fig. 6b, curves III and IV). The high temperatures in the *Scirpus* chamber were due to the location of the remote blower in the warmest section of the *Scirpus* canopy.

Air temperature was also monitored with a single thermocouple inside all of the *Spartina*, two of the *Scirpus* and two of the mixed chambers.

Outside air temperature was monitored at two locations in each community. Measurements of air temperature were made above the plant canopy in the *Spartina* and mixed communities and within the top of the plant canopy in the *Scirpus* community. A summary of differences between air temperature inside and outside the chambers ($T_i - T_o$) during 1987 is given in Table 2. $T_i - T_o$ ranged from 1.5 to 1.9°C in open top chambers over 24 h. Midday $T_i - T_o$ was slightly higher, ranging from 1.2 to 2.7°C. The greatest temperature differences were in the *Scirpus* community.

Reported temperature increases inside large open top chambers were about 2°C and occurred at midday on warm, sunny days (Heagle *et al.*, 1973, 1979; Mandl *et al.*, 1973; Olszyk *et al.*, 1980), although Weinstock *et al.* (1982) observed increases as great as 3.7°C. Night-time differences were near 0°C. Therefore, increased T_i was attributed to radiant heating by the chamber (Unsworth, 1982; Weinstock *et al.*, 1982). Olszyk

Table 2. Air temperature differences ($T_i - T_o$, °C) in open top chambers from the three marsh communities. Temperatures were averaged between 1000 and 1400 h (mid day) and 0000 and 2400 h (24 h). Mean \pm SD (n).

	<i>Spartina</i>	Mixed	<i>Scirpus</i>
24 h	1.9 \pm 0.4 (124) ⁺	1.5 \pm 0.6 (38)	1.9 \pm 0.7 (38)
Mid day	2.1 \pm 1.2 (124)	1.2 \pm 1.4 (38)	2.7 \pm 1.9 (38)

⁺ Each observation is the average of all measurements on one day for a single chamber.

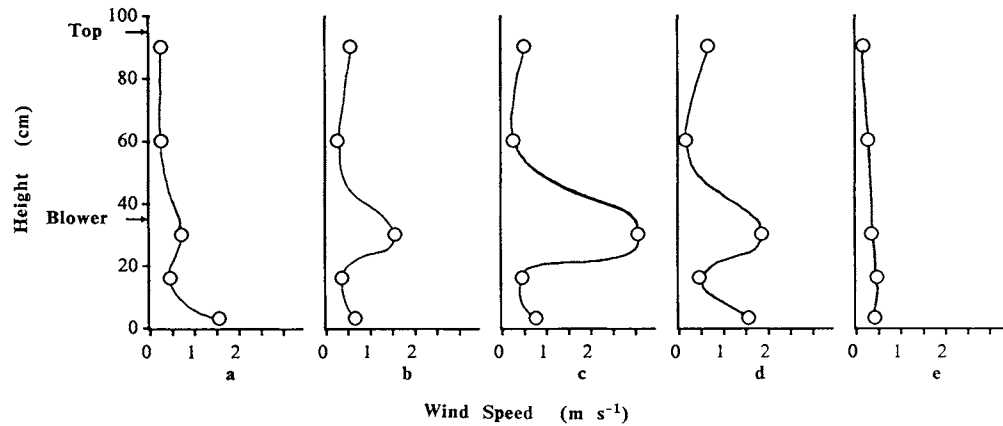


Fig. 5. Vertical profile of wind speeds at five locations (a–e) inside an open top chamber. Chamber was empty and was sealed at the bottom.

et al. (1980) attributed a 1°C increase in early morning T_i to a ground level inversion outside the chamber. Our data indicated T_i was a complex function of naturally occurring temperature profiles, location of the air inlet of the chamber, location of air from the mixing blower into the chamber, heating by blowers, disruption of the vegetation boundary layer and radiant heating.

Vegetation temperature

Air temperature is an important factor in the energy budget of vegetation but physiological processes such as photosynthesis and respiration are directly dependent on tissue temperature. In the mixed and *Spartina* communities, vegetation $T_i - T_o$ was approximately the same as air $T_i - T_o$. In the *Scirpus* community, differences between air $T_i - T_o$ and vegetation $T_i - T_o$ of 1–4°C were recorded. The average daytime vegetation $T_i - T_o$ for 5 days in June 1987 was *c.* 1.5°C. Similar results were reported by Weinstock *et al.* (1982) using thermocouples attached directly to leaf surfaces.

Effects on vegetation

There was no difference between plant growth in the ambient chambers and the unchambered controls for the *Spartina* and mixed communities (Table 3). However, plants from ambient chambers in the *Scirpus* community showed greater shoot density and later senescence than those in unchambered control sites (Curtis *et al.*, 1989).

There are several possible reasons for this chamber effect on *Scirpus* growth in the *Scirpus* community but not in the mixed community. First, air temperature inside chambers in the *Scirpus* community was slightly higher than the air temperature in the mixed community. Second, there was considerably more physical damage to the plants surrounding the *Scirpus* chambers than the mixed chambers because pure *Scirpus* stands were very sensitive to trampling. More light was available from the side in the chambered sites in the *Scirpus* community since the area surrounding the chambers suffered more damage than the area surrounding the control sites due to the additional traffic to the chambered sites for maintenance

Table 3. Standing dry weight and shoot density of *Scirpus* from the *Scirpus* and mixed communities in September and of the *Spartina* community in August, 1987. Mean (SE), $n = 5$ chambers per treatment per community.

	Elevated	Ambient	Control
Dry weight (g m ⁻²)			
<i>Scirpus</i> - <i>Scirpus</i>	899 (108) ^{a+}	715 (103) ^b	381 (43) ^c
<i>Scirpus</i> -mixed	160 (30) ^a	72 (15) ^b	55 (11) ^b
<i>Spartina</i> - <i>Spartina</i>	588 (27) ^a	577 (56) ^a	624 (55) ^a
Shoot density (shoots m ⁻²)			
<i>Scirpus</i> - <i>Scirpus</i>	802 (98) ^a	610 (82) ^b	292 (49) ^c
<i>Scirpus</i> -mixed	215 (36) ^a	78 (19) ^b	101 (14) ^b
<i>Spartina</i> - <i>Spartina</i>	5250 (170) ^a	5730 (480) ^a	6510 (750) ^a

^a Similar superscript indicates no significant difference, $P < 0.05$.

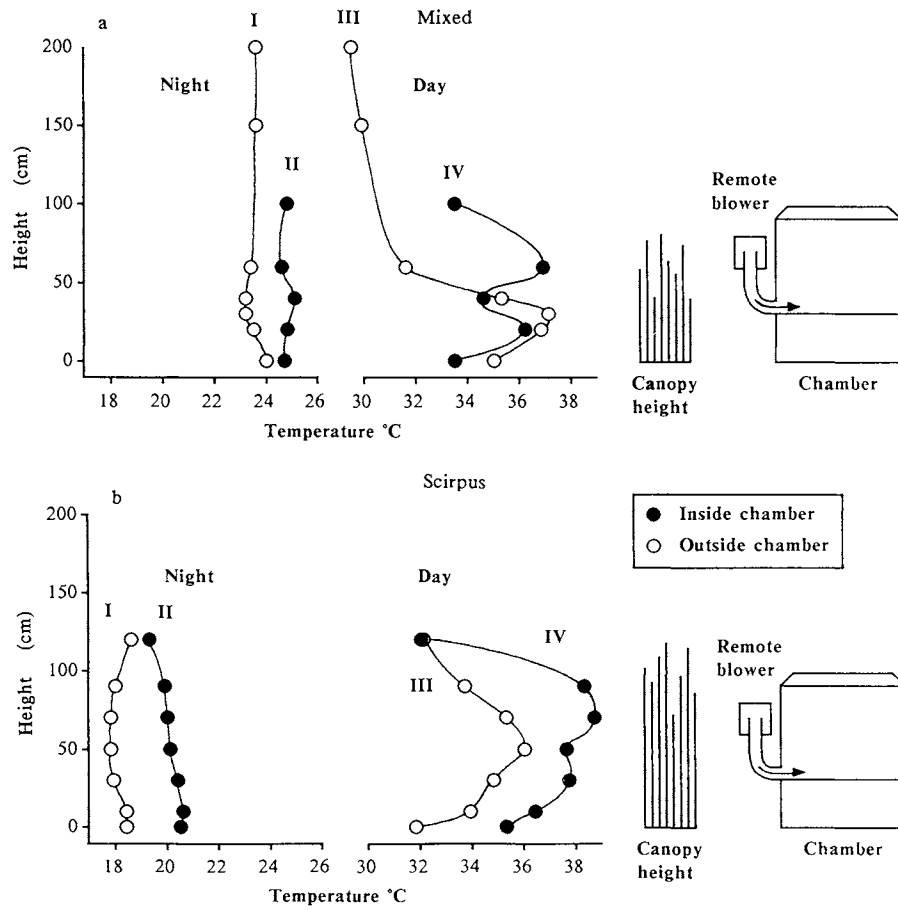


Fig. 6. Vertical profiles of air temperatures outside (○) and inside (●) an open top chamber in the mixed (a) and *Scirpus* (b) communities. Night temperatures (curves I and II) were taken at 0300h and day temperatures (curves III and IV) at 1400h. The canopy and chamber illustrations are drawn to scale with the vertical axis to show the location of the remote blower and the inlet to the chamber.

work. Third, the chambers also gave physical protection to individual *Scirpus* stems, which reduced wind damage inside the chambers in the *Scirpus* community. This protection was less important in the mixed community where *Scirpus* was protected by the surrounding grasses. Decreased or increased yield (Howell, Kock & Rose, 1979; Heggstad *et al.*, 1980), greater plant height (Heagle *et al.*, 1973, 1979) and delayed senescence (Weinstock *et al.*, 1982) have been observed in large open top chambers. Such chamber effects may be unavoidable but we hope to reduce their magnitude in the *Scirpus* community by changing the source, and hence the temperature, of air blown into the chambers and by reducing damage to the area surrounding the chambers.

Conclusions

The open top chamber described here has proven to be adequate for the most important task for

which it was designed: generation of test atmospheres of elevated CO_2 around plants growing in the field. The effect of the chamber on micro-environment was similar to the effects of large open top chambers used in research on agricultural species. Perturbations of the micro-environment by open top chambers may alter plant growth but the available alternatives for elevation of CO_2 *in situ* also have liabilities. Refinement and improvement of the open top chamber is a goal of this project with the ultimate aim of reducing the effects of these chambers on micro-environment and plant growth.

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