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Progress Report of Research: EFFECTS OF ELEVATED CO_2 ON CHESAPEAKE BAY WETLANDS. III. Ecosystem and Whole Plant Responses in the First Year of Exposure, April-November 1987.

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EXECUTIVE SUMMARY

Open-top chambers were used to raise CO_2 concentrations ca. 340 ppm above ambient over monospecific communities of Scirpus olneyi (C_3) and Spartina patens (C_4), and a mixed community of Scirpus, Spartina, and Distichlis spicata (C_4) on a Chesapeake Bay brackish marsh. Mean annual CO_2 concentrations were 350 ± 22 ul l^{-1} in chambers which received no added CO_2 and 686 ± 30 ul l^{-1} in chambers with elevated CO_2 concentrations. A summary of our major findings is as follows:

1. During spring and early summer, net ecosystem CO_2 assimilation of the Scirpus community grown in elevated CO_2 was 50% greater than canopies grown in normal ambient CO_2 concentration. In the Mixed and Spartina canopies grown in elevated CO_2 the response was only about 10% more than in the canopies grown at normal ambient CO_2 concentrations. After mid July, however, the relative enhancement of canopy photosynthesis increased in all three communities and in the Scirpus community, the relative improvement in carbon dioxide assimilation during September and October exceeded 100%. Photosynthesis of single leaves of Scirpus, measured in mid season, was higher in plants grown in elevated CO_2 than in plants grown at normal ambient CO_2 concentrations. Leaves of Spartina had no higher photosynthesis rates in elevated CO_2 than in normal ambient CO_2 concentrations. Elevated CO_2 resulted in an increase in carbon sequestering of 25% in the C_4 plant community and 106% in the C_3 community.

2. Elevated CO_2 resulted in increased shoot densities and delayed senescence in the C_3 species in pure stand and in the Mixed community. This resulted in an increase

in primary productivity in Scirpus growing in both the pure and mixed communities. There was no effect of CO_2 on growth in either of the two C_4 species.

3. Green shoot nitrogen concentration was reduced and carbon concentration was unchanged under elevated CO_2 which resulted in a 20%-40% increase in tissue C/N ratio in Scirpus. There was no effect of the CO_2 treatment on the C/N ratio in either C_4 species. Elevated CO_2 did not change total aboveground nitrogen (g/m^2) in the Scirpus community because increased production compensated for decreased tissue nitrogen. There was no change in the N recovery efficiency of Scirpus in pure stand but there was a decrease in the elevated CO_2 treatment in the mixed community. Litter C/N ratio was not affected by elevated CO_2.

4. Midday shoot water potentials were significantly higher in all three species under elevated CO_2. This was found in both field and laboratory grown plants. Preliminary data show that reductions in evapotranspiration in both C_3 and C_4 canopies contributed to an approximate doubling in water use efficiency.

5. The open top chamber functioned very well in maintaining test atmospheres and, in the closed top configuration, for the measurement of net ecosystem gas exchange. Air temperatures inside the chamber averaged 2 C above ambient outside the chamber.

These results demonstrate that a doubling in atmospheric CO_2 concentration can have important ecological consequences. In a single year, photosynthesis, growth and nitrogen nutrition were altered in the C_3 component of the high marsh. Water relations were improved for all species studied. If these responses are sustained over time we can expect profound changes in the structure and functioning of this brackish marsh. But there is no way to know whether they will be sustained and predictions concerning long term ecosystem behavior based on a single year's data will have considerable uncertainty surrounding them.

For example, some of our data suggest that nitrogen available to the canopy for growth of new photosynthetic tissue could limit future growth increases in Scirpus. However, increased carbon allocation to roots and a larger belowground nitrogen pool, for which we have some evidence, could substantially change this.

Net canopy CO_2 uptake and plant water relations improved in Spartina as the season progressed, but we saw no increase in aboveground growth. Thus, a delayed response in this perennial species which has large belowground carbon reserves is not at all unlikely.

Completing detailed carbon and nitrogen budgets for the three communities under study will improve our predictive abilities. A principal need in this endeavor will be more complete information on belowground processes. It is in this area that carbon supply and nitrogen availability interact. The consequence of this interaction may well determine the long term consequences of elevated CO_2 to the brackish marsh. There is no question that the perennial plants in this ecosystem will respond to elevated CO_2 but it is too soon to tell how this will affect such ecosystem processes as carbon sequestering, nutrient dynamics, species composition, or water balance.

INTRODUCTION

The steady rise in atmospheric carbon dioxide concentration has prompted considerable research concerning the likely consequences of this anthropogenic change on plant growth (reviewed in Strain and Cure 1985). Most of this work has been conducted with agricultural species under laboratory or controlled field conditions. Despite our improved understanding of the physiology of the CO_2 response, it has been difficult to extrapolate from this work to unmanaged plant communities. The great diversity in growth responses among annual species to elevated CO_2 (Carlson and Bazzaz 1980; Kimball 1983), the paucity of long term research, and the important influence of environmental stress in the CO_2 response (Patterson and Flint 1982; Bowman and Strain 1987) all make very uncertain any predictions concerning the response of a specific ecosystem to this global climate change.

Results from studies of agricultural species and, to a lesser degree, wild species have led to several general hypotheses regarding ecological responses to elevated CO_2. Plants with the C_3 pathway of photosynthesis usually increase carbon assimilation and growth in response to increases in CO_2 concentration (Ford and Thorne 1967; Rogers et al. 1983; Downton et al. 1987) whereas C_4 plants are more variable and generally respond less than C_3 plants (Carlson and Bazzaz 1980; Potvin and Strain 1985; Smith et al. 1987). In communities containing C_3 species, net primary productivity should therefore increase, and C_3 species may gain a competitive advantage over C_4 species (Carter and Peterson 1983; Zangerl and Bazzaz 1984). Both C_3 and C_4 plants show an increase in water use efficiency under elevated CO_2 (Morison 1985). This could have a significant effect on water availability in arid and mesic environments (Wigley and Jones 1985). Low nutrient availability tends to decrease the relative response to CO_2, but the opposite is true for water stress. In environments where plant growth is strongly controlled by one of these limiting factors (e.g. coniferous forests, deserts), the magnitude of the response should vary accordingly (Oechel and Strain 1985).

To date, only one study has involved an unmanaged plant community that was exposed to elevated CO_2 *in situ* for an entire growing season (Oechel et al. 1984). In an arctic tussock sedge ecosystem, Oechel and co-workers found that canopy and single leaf photosynthesis increased substantially in the first year of exposure to a doubling of CO_2 but that acclimation occurred and by the fourth year there was no detectible difference between elevated and control plots. There was no effect on net productivity although the sedge *Eriophorum vaginatum* showed an increase in tillering (Tissue and Oechel 1987). These results suggested that in the arctic, sustained community level responses to increased atmospheric CO_2 would not occur.

We have used a modified open top chamber in the field to study the effects of increased CO_2 concentration on unmanaged wetlands vegetation. Here we report results from the first year of exposing a temperate salt marsh ecosystem to a doubling of atmospheric CO_2 concentration. Three high marsh communities containing monospecific populations of C_3 and C_4 species, and these same species in combination were studied. The co-occurrence of C_3 and C_4 dominants and high system productivity make salt marshes ideal environments in which to test current theories of ecosystem responses to CO_2. Salt marshes also accrete large amounts of carbon annually (Haines and Dunn 1985) and may thus be important sinks for atmospheric CO_2.

Treatment with elevated CO_2 began in April and continued into november 1987. Photosynthesis of leaves and of canopies, numbers of shoots and biomass of belowground roots and rhizomes, tissue nitrogen and carbon content, and plant water potential were followed to assess the effect of the elevated CO_2 treatment on ecosystem processes.

Elevated CO_2 increased photosynthesis in leaves of the C_3 sedge Scirpus olneyi but not in the C_4 grass Spartina patens. There was no evidence of acclimation of photosynthesis to elevated CO_2 in the C_3 grass. There was evidence of some acclimation of photosynthesis in the C_4 grass Spartina patens and this was seen as a decline in photosynthesis at elevated CO_2 compared with ambient CO_2. However, this effect was small.

In monospecific stands of the C_3 sedge, Scirpus olneyi, during early summer elevated CO_2 increased canopy photosynthesis by about 50% above photosynthesis in canopies kept at ambient CO_2 concentration. In the mixed community and in the monospecific stands of the C_4 grass, Spartina patens, elevated CO_2 only increased photosynthesis by about 10% throughout the early part of the growing season. After mid-July, however, the effect of elevated CO_2 on photosynthesis increased in all three communities and by September photosynthesis in the C_3 community was improved over 100% by the CO_2 treatment. An interesting finding was that in late summer and fall, elevated CO_2 had a very large relative effect on the C_4 grass community even though the data on single leaf photosynthesis showed no significant effect of CO_2. There were effects of elevated CO_2 on development and on canopy architecture which were not anticipated from studies of single plants and which have a significant effect on carbon sequestering. These effects are not understood but are the subject of ongoing research. The data are discussed and an interpretation is offered in Chapter 3 on photosynthesis.

We obtained evidence for the strong involvement of environmental factors in the CO_2 response in plant communities. Temperature had a large effect on the daytime relative effect of elevated CO_2 on canopy photosynthesis in the monospecific stands of the C_3 sedge. Above 39C the rise in photosynthesis in plants grown in elevated CO_2 compared with those grown in ambient CO_2 was very steep. At 37 C photosynthesis in elevated CO_2 was about 25% greater than in normal ambient CO_2 but the improvement rose to 80% at 44 C. Light also increased the relative effect of elevated CO_2 in the C_3 sedge but had no effect in either the mixed community or the C_4 grass community.

The most pronounced effect of the doubling in ambient CO_2 concentration on growth in these salt marsh communities was an increase in shoot numbers and decrease in the rate of senescence in the C_3 sedge, Scirpus olneyi. This resulted in a significant increase in live, aboveground biomass in the latter half of the season and greater net primary productivity in Scirpus from both the SCIRPUS and MIXED communities. These results support the prediction that plant growth in mature, unmanaged ecosystems containing C_3 species will increase in response to increasing atmospheric CO_2 concentrations (Bazzaz et al. 1985). We found no growth response in the SPARTINA community or the C_4 component of the MIXED community.

The increased shoot growth by Scirpus in the MIXED community did not have any detectible negative effect on Spartina and Distichlis but the long term consequences of a sustained growth response by Scirpus in this community are difficult to predict. Regions of the marsh with vigorous Scirpus populations have very little Spartina or Distichlis present. Competition as well as edaphic conditions are probably important in determining local species abundances on salt marshes (Snow and Vince 1984).

The slower rate of senescence and continued production of new shoots in Scirpus under elevated CO_2 resulted in a greater number of green shoots present in September and October, a slower relative rate of decline in aboveground biomass, and a lower percentage senescent tissue present in November.

The chambers had a significant effect on growth in the SCIRPUS community although there was no effect on Scirpus from the MIXED community or on the C_4 species. The 2^{o} C temperature increase, protection of shoots from mechanical damage, and possibly higher humidity inside chambers could have contributed to the observed effects on growth.

We found a clear dichotomy in the effects of elevated CO_2 on shoot N in the C_3 and C_4 species. Increasing CO_2 reduced green tissue N in Scirpus but had no effect on Spartina or Distichlis. We found no evidence for increased carbon in Scirpus shoots although there were increases in both canopy and single leaf photosynthesis under elevated CO_2. This suggests that belowground rhizomes provided adequate sinks for the increased assimilation. Scirpus also showed no signs of photosynthetic acclimation or inhibition to elevated CO_2. The reduction in %N of Scirpus shoots resulted in an increase in green tissue C/N ratios of between 20 and 40%. Scirpus appears to preferentially allocate N into seeds since both the green shoots supporting the inflorescences and the bracts enveloping the seeds had lower N under elevated CO_2 but there was no reduction in seed N.

We found no evidence that exposure to elevated CO_2 led to an increase in total aboveground N. Rather, it appears that increased productivity in Scirpus under elevated CO_2 came at the expense of lower shoot N. While results from the first year of a long term study such as this can only indicate trends in ecosystem level processes, our data suggest that total N available for aboveground growth, and hence tissue N, may limit the potential for increases in productivity due to CO_2. We cannot at present say, however, to what extent N may be limiting current productivity.

Scirpus did not respond to the reduction in leaf N by increasing N recovery efficiency. In pure stand, Scirpus had a recovery efficiency of approximately 70%, similar to the maximum of 66% reported by Shaver and Mellilo (1984) for three marsh species grown at limiting available N, but there was no effect of CO_2. Recovery efficiency was lower in the mixed community where Scirpus was heavily shaded by Spartina and Distichlis and light may have been more important in limiting growth than N availability. Elevated CO_2 further reduced recovery efficiency in the mixed community resulting in more N lost in litter.

Midday shoot water potential was significantly higher in all 3 species under elevated CO_2, whether grown in the field or in the laboratory. Laboratory grown plants showed a decrease in water use per shoot while field grown plants had reduced transpiration and increased water use efficiency under elevated CO_2. An increase in water use efficiency through a combination of reduced transpiration and increased photosynthesis is perhaps the most general response of plants to elevated CO_2. Our data suggest that the stomatal response to high CO_2 might be even greater in the C_4 species than in the C_3. This improvement in water relations in the two C_4 species did not translate into improved growth during this first season.

CHAPTER 1

FURTHER DEVELOPMENT AND TESTING OF THE CO_2 EXPOSURE SYSTEM

In greenbook 038 (Drake et al. 1987) we reported microclimatic data from inside open and closed top chambers (Fig 1.1) during preliminary field testing in the summer of 1986. In this chapter we present much more extensive results of chamber performance and effects on microclimate obtained after a full season of use in 1987. In 1986, only three chambers received elevated CO_2 for approximately 4 months. In 1987, fifteen chambers received elevated CO_2 for the entire growing season from mid April to early November. In addition to collecting data on the maintenance of test atmospheres we also monitored variations in normal ambient CO_2 concentrations both temporally and along a vertical profile.

We also expanded our recording of the thermal environment. We present here seasonal data on temperatures inside and outside open and closed top chambers from single point measurements. Detailed temperature profiles were also constructed during mid-summer. As in 1986, air temperatures measured with thermocouples were compared with vegetation temperatures measured with a hand held infra-red thermometer.

CO_2 Concentration - The most important task of the open top chamber was to generate test atmospheres of elevated CO_2 concentration. A 24 hour record of CO_2 concentration inside an Ambient and an Elevated chamber is shown in Figure 1.2. The difference in CO_2 concentration between Ambient and Elevated chambers remained virtually constant throughout the day and night. Seasonal mean daytime CO_2 concentrations from each of the three communities are given in Table 1.1 and from each chamber in Table 1.2. Average CO_2 concentrations in Elevated chambers were maintained close to 340 ul l^{-1} above ambient concentration, but

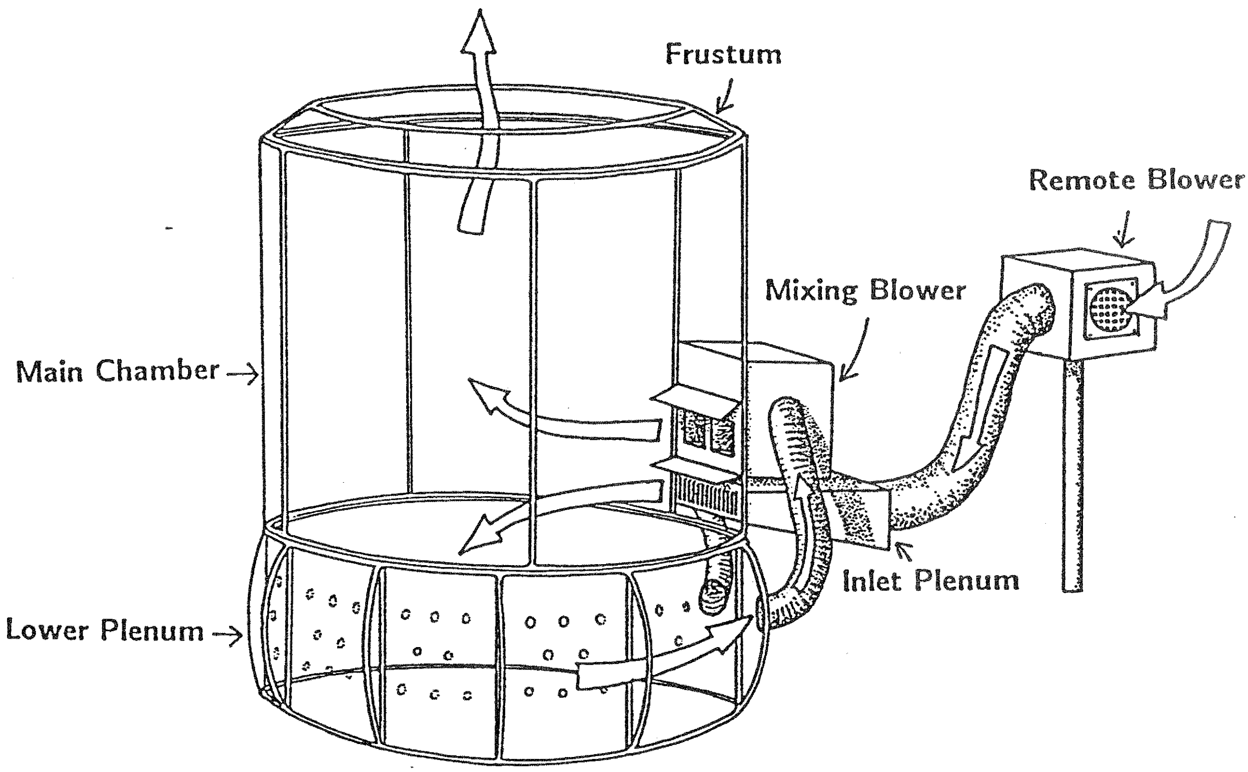


Figure 1.1. Open top chamber detailing flow of air. Air is drawn into the remote blower and blown through the inlet plenum into the chamber. The mixing blower draws air from inside the chamber through the perforated inner wall of the lower plenum and blows it back into the chamber. Air exits the chamber through the frustum.

the variability in CO_2 concentration increased during windy periods. For example, on a day with winds averaging 1.2 m s^{-1}, CO_2 concentrations in the Elevated chambers were 336 $\pm$ 16 ul l^{-1} above ambient concentrations. On a day with winds averaging 4.3 m s^{-1}, CO_2 concentrations were 355 $\pm$ 53 ul l^{-1} above ambient concentrations.

Figure 1.3 shows profiles of ambient CO_2 concentration above the marsh surface during the day and at night in the Scirpus community. CO_2 concentrations were relatively constant with height during midday (Fig 1.3, curve A) with average CO_2 concentrations below 350 ul l^{-1} and very slight depressions in CO_2 concentration in the middle of the canopy. On windy nights CO_2 concentrations were also relatively constant and only slightly higher than during midday (Fig 1.3, curve B). On very still nights (Fig 1.3, curve C) there were steep gradients in CO_2 concentration with the highest concentrations measured at the bottom portion of the canopy. During such nights, ambient CO_2 concentrations at ca. 1 m was as high as 1200 ul l^{-1}. A complete diurnal profile of CO_2 concentration in the Scirpus community with the corresponding wind speeds is shown in Figure 1.4. The seasonal change in CO_2 at 70 cm above the marsh is shown in Figure 1.5.

The high CO_2 concentrations shown in Figure 1.3, curve C were not caused by CO_2 supplied to Elevated chambers since the CO_2 supply was interrupted during these measurements. Rather, they were likely due to the accumulation of respiratory CO_2 evolving from the marsh sediments, marsh vegetation, or the adjacent forest. The marsh was surrounded on three sides by forested uplands, forming a natural basin for CO_2.

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 1.6). At night, air temperature outside the chamber (T_o) was lowest at

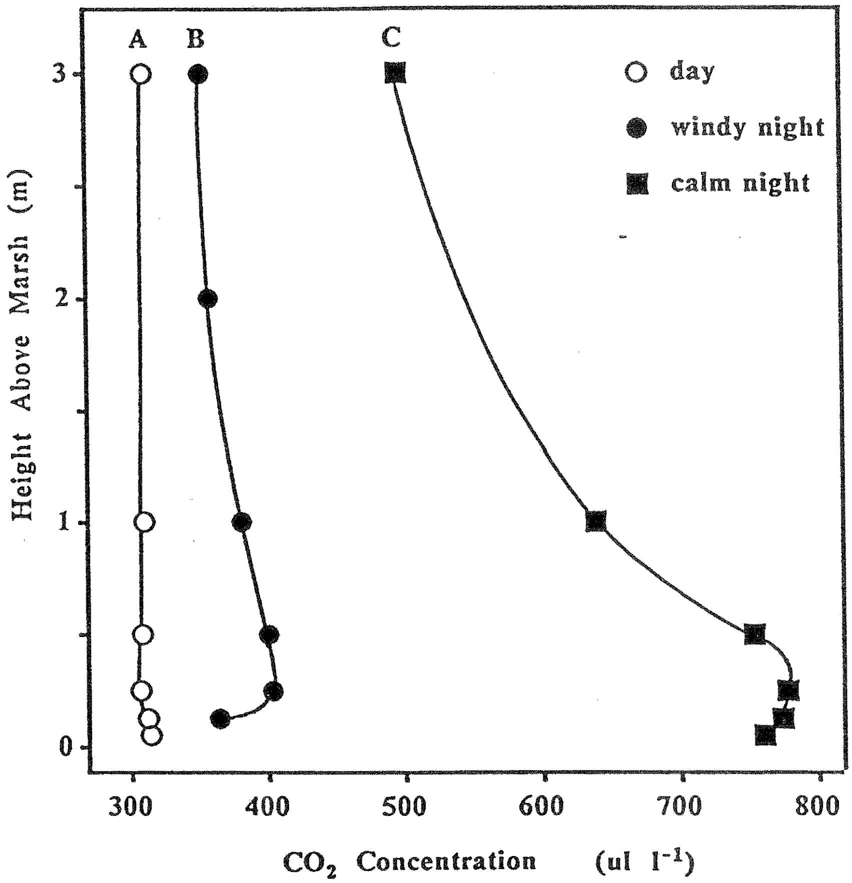


Figure 1.3. CO_2 profiles above the marsh in the Scirpus community during the day (curve A) and on a windy (curve B) and calm night (curve C). CO_2 concentrations were recorded at 30 sec intervals and averaged over a single 15 min period in each profile. Measurement dates were August 18 (A,C), and August 24 (B), 1987.

Table 1.1. Daytime (sunrise to sunset) mean CO_2 concentration in Elevated and Ambient chambers from the three marsh communities. Mean ± S.D. (N).

	[CO2] ($ul\ l^{-1}$)
Elevated	
Spartina	683 ± 29 (844)[+]
Mixed	686 ± 31 (855)
Scirpus	688 ± 31 (844)
Pooled	686 ± 30 (2543)
Ambient	
Pooled	350 ± 22 (169)

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

Table 1.2. Seasonal absolute CO_2 concentrations inside Elevated chambers from each community and target CO_2 concentrations (Elevated - Ambient). Mean $\pm$ (s.d.),N.

Chamber	24 hr	Day
	ppm CO_2	
Mx 1 E	717 (46),165	686 (28),170
Mx 4 E	706 (55),167	678 (39),171
Mx 8 E	733 (54),166	696 (28),171
Mx 11 E	724 (51),167	686 (29),172
Mx 13 E	709 (46),165	683 (30),171
Target (Mixed)	330 (43),835	336 (29),835
Sc 1 E	733 (56),166	689 (28),168
Sc 6 E	725 (49),166	687 (30),171
Sc 9 E	733 (55),167	691 (28),168
Sc 10 E	725 (47),166	686 (26),168
Sc 14 E	792 (64),166	687 (39),169
Target (Scirpus)	340 (41),821	337 (28),820
Sp 1 E	712 (50),167	684 (28),166
Sp 4 E	710 (53),167	680 (39),169
Sp 8 E	712 (46),167	683 (26),171
Sp 10 E	722 (45),167	686 (25),171
Sp 14 E	717 (54),166	686 (28),167
Target (Spartina)	326 (25),820	334 (25),825

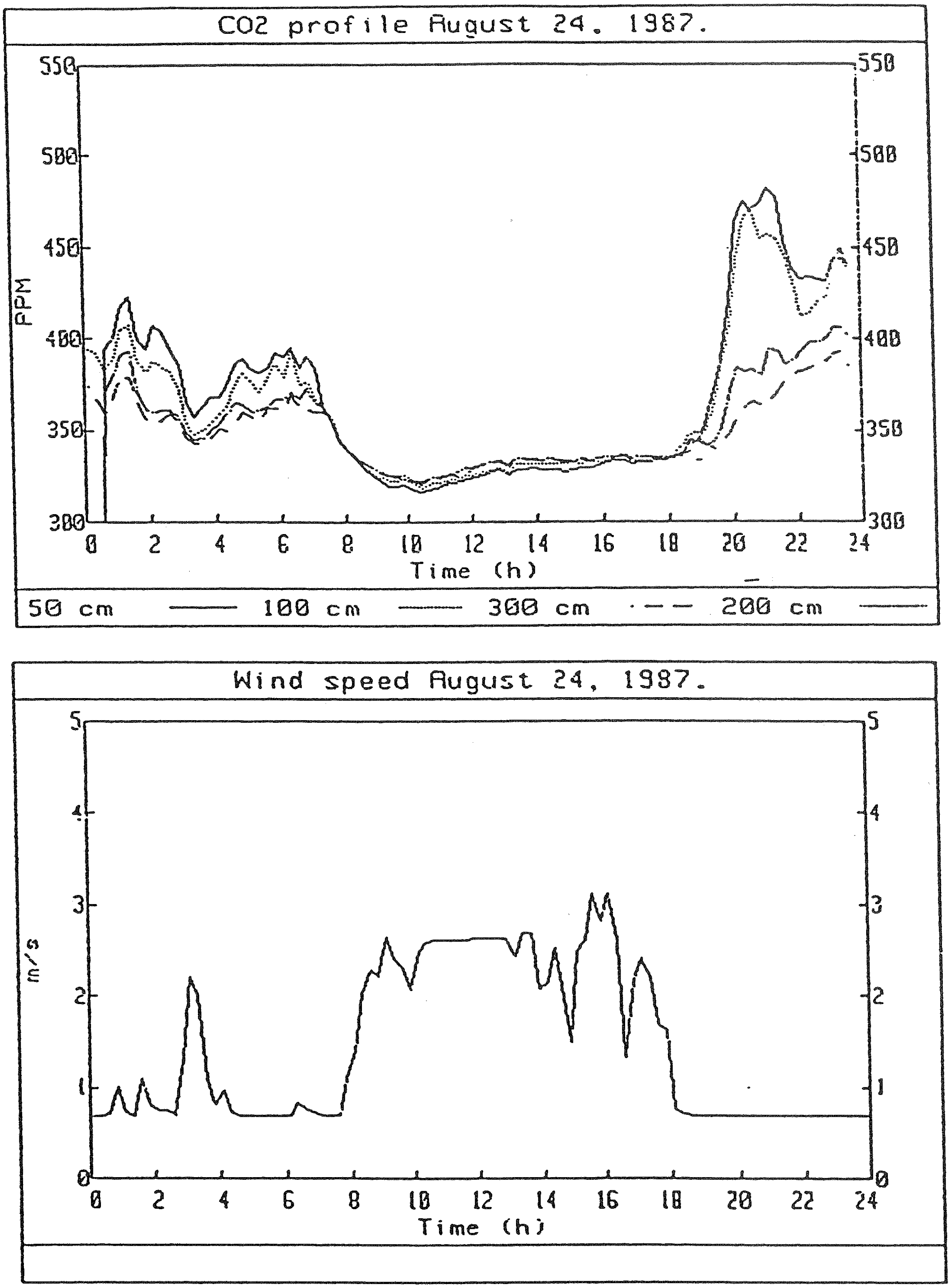


Figure 1.4. A. Diurnal time course of CO_2 concentrations above marsh surface at four heights showing effect of varying wind speed B. Wind speed at 3 m above marsh.

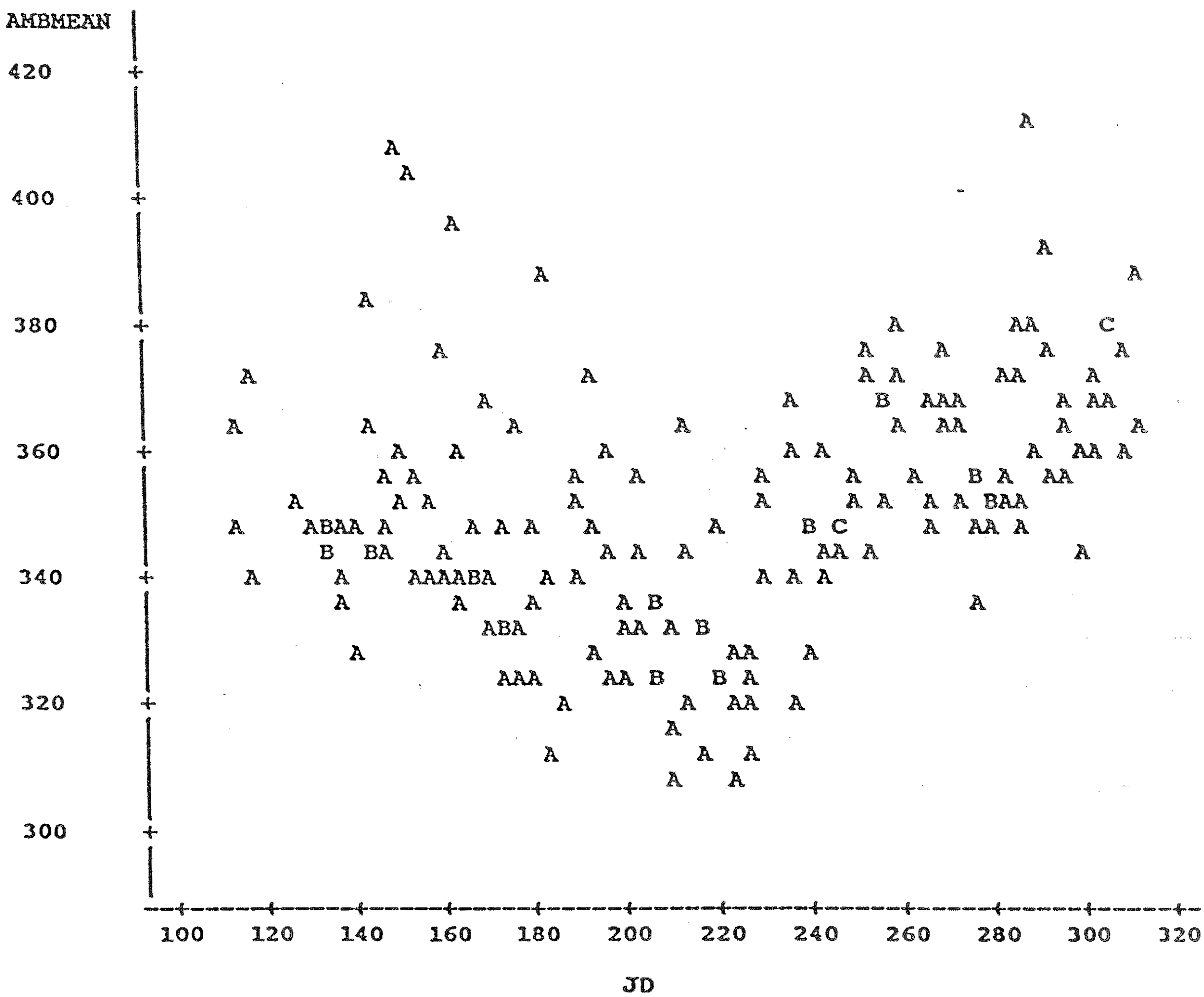
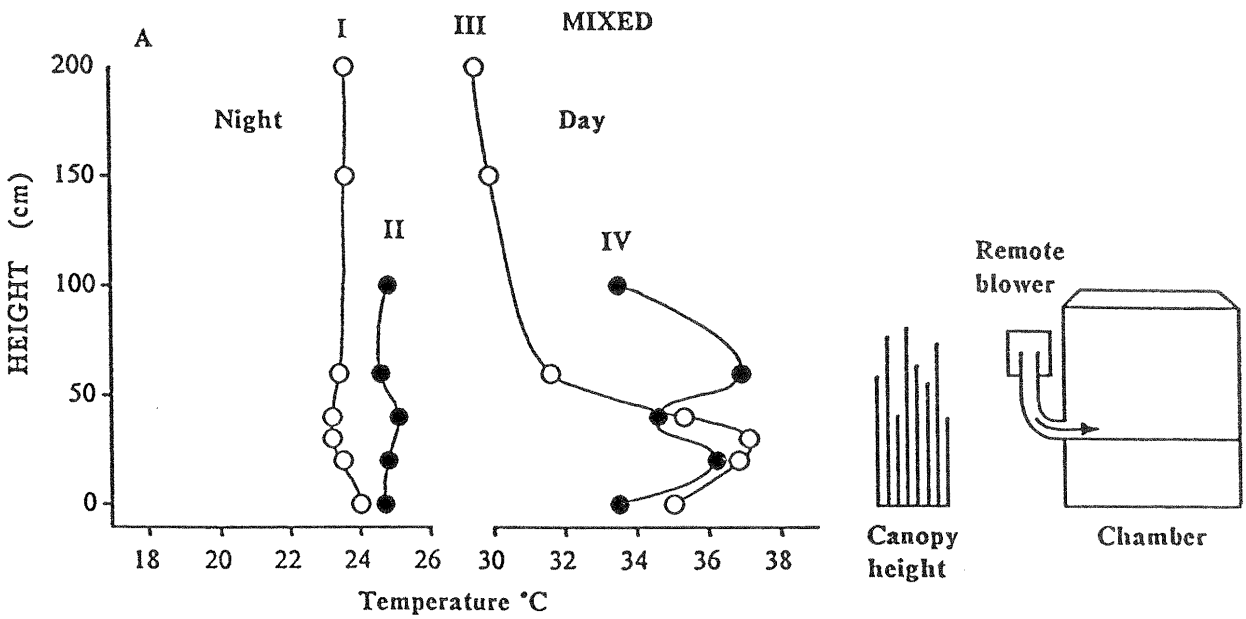


Figure 1.5. Seasonal course of mean diurnal ambient CO_2 concentrations sampled 70 cm above marsh surface.

about 40 cm in the Mixed community, and between 30 and 80 cm in the Scirpus community (Fig 1.6A & 1.6B, curve I). The shape of this profile is characteristic of an inversion condition. Air temperature inside the chambers (T_i) at night was 1-2 C higher than T_o (Fig 1.6A & 1.6B, curve II). Thermocouples placed before and after the remote and mixing blowers demonstrated that each blower raised air temperatures about 1.2 C (Drake et al. 1987), indicating that much of the increase in temperature inside the chamber at night could be explained by heating by the blowers.

During the day, temperature profiles outside the chambers (Fig 1.6A & 1.6B, curve III) were typical of lapse conditions. In the Mixed community, T_o was lowest above the canopy and increased downward toward the marsh surface (Fig 1.6B, 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 1.6B, 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, and then drawn into the lower plenum and reintroduced into the chamber at 0.5 m (compare the chamber illustration in Figure 1.6B with curves III and IV). Temperature profiles in the Scirpus community were similar to those in the Mixed community except that the entire profile inside the Scirpus chamber was warmer than outside by 2-4 C (Fig 1.6A, 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. This has been changed by elevating the blower above the canopy. A more detailed time course of these temperature profiles is presented in Figure 1.7 (Scirpus community) and Figure 1.8 (Mixed community).



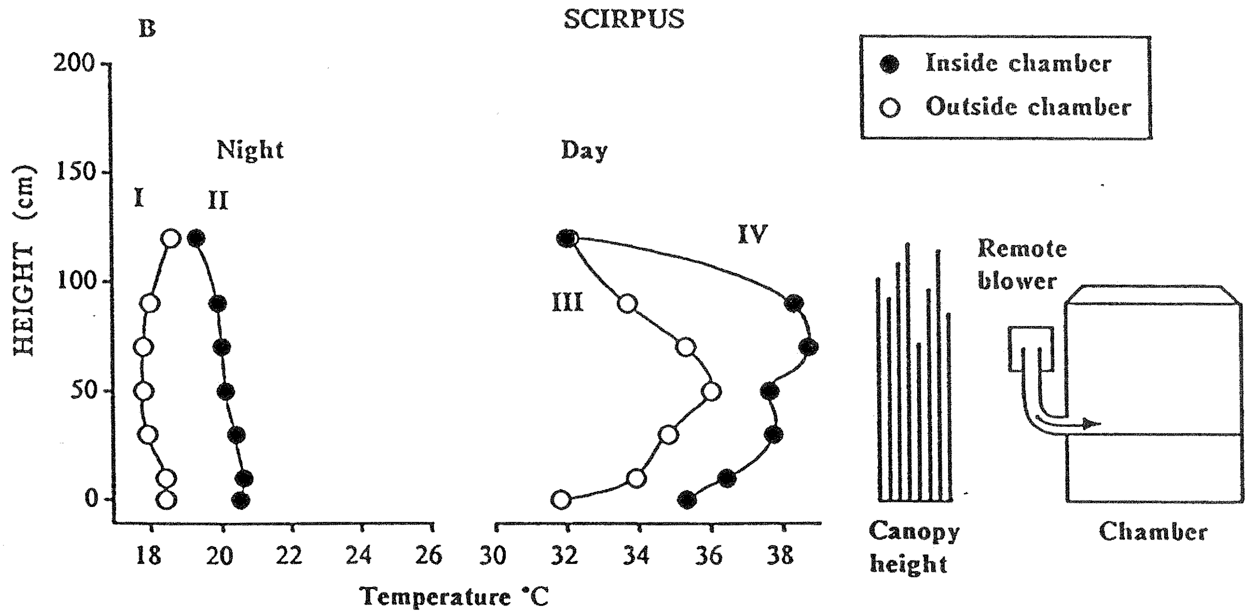


Figure 1.6. Vertical profiles of air temperatures outside (O) and inside (●) an open top chamber in the Mixed (A) and Scirpus (B) communities. Night temperatures (curves I and II) were taken at 3:00 and day temperatures (curves III and IV) at 14:00. The canopy and chamber illustrations are drawn to scale with the vertical axis.

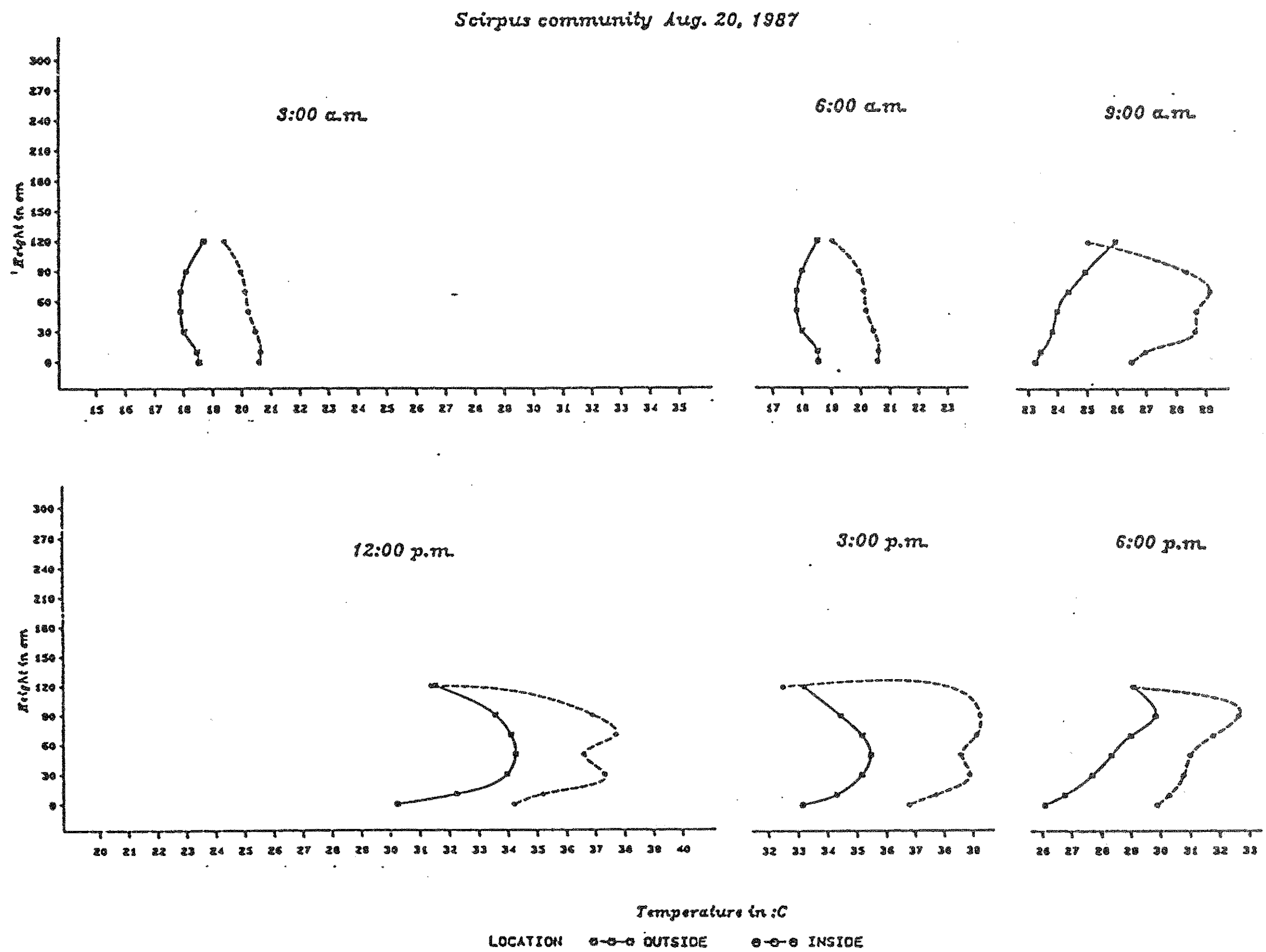


Figure 1.7. Temperature profiles inside a Scirpus open top chamber on a single day from 3:00 am to 6:00 pm.

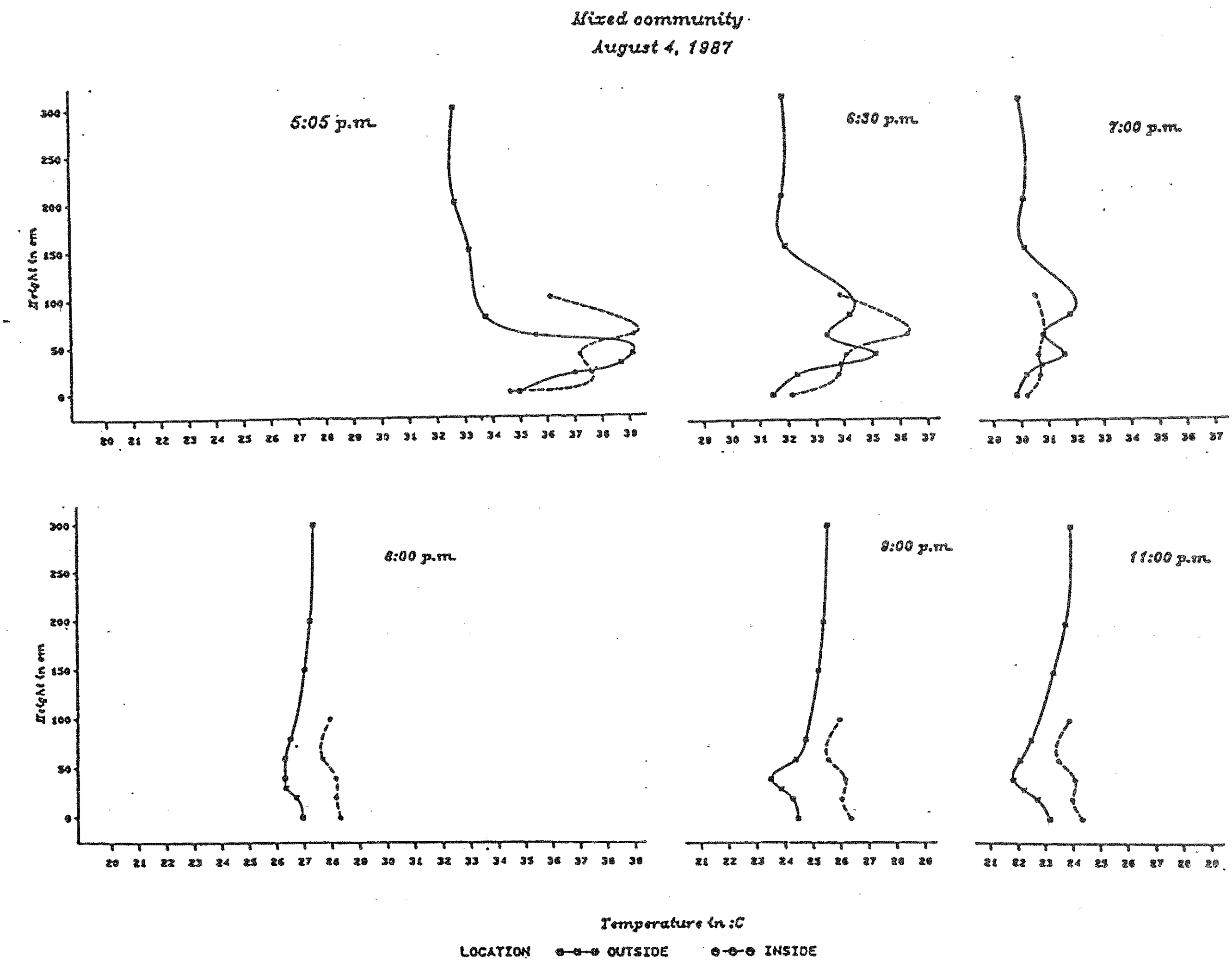


Figure 1.8. Temperature profiles inside a Mixed open top chamber on a single day from 5:05 pm to 11:00 pm.

Air temperature was also monitored with a single thermocouple inside all of the Spartina (Table 1.3), 2 of the Scirpus (Table 1.4), and 2 of the Mixed chambers (Table 1.5) throughout the 1987 season. Outside air temperature was monitored at 2 locations in each community (Fig 1.9). Measurements of air temperature were made above the top of 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 1.6. T_i - T_o ranged from 1.5 to 1.9 C in open top chambers over 24 hrs. Midday T_i - T_o was slightly higher, ranging from 1.2 to 2.7 C. The greatest temperature increases were in the Scirpus community. 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 exhaust into the chamber, heating by blowers, disruption of the vegetation boundary layer, and radiant heating.

Air temperatures in closed top chambers increased relative to open top chambers by 0.5 C over 24 hours and by 1.1 C during midday (Table 1.6). The greatest difference was in the Scirpus community, where midday T_i - T_o was 3.7 C. To minimize the effect on the vegetation of the increase in temperature, chambers were used in the closed top configuration briefly, usually 3-4 days, and then converted to the open top configuration for periods of 2-4 weeks.

Table 1.3. Seasonal course of temperatures inside (Ti) and outside (To) open and closed top chambers in the Spartina community. Data are mean values for entire 24 hr periods or during four hours of midday (10:00-14:00).

MIDDAY TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
148	Sp 10 E	32.4	28.9	3.55
148	Sp 11 A	33.1	28.9	4.26
158	Sp 10 E	36.4	34.3	2.07
158	Sp 11 A	33.4	34.3	-.94
185	Sp 1 E	36.7	32.3	4.45
185	Sp 2 A	35.7	32.3	3.44
185	Sp 4 E	35.7	32.3	3.45
185	Sp 5 A	35.9	32.3	3.62
185	Sp 9 A	36.3	32.3	4.01
185	Sp 8 E	36.7	32.3	4.41
185	Sp 10 E	35.9	32.3	3.65
185	Sp 13 A	36.4	32.3	4.14
189	Sp 1 E	39.0	34.5	4.51
189	Sp 2 A	38.0	34.5	3.53
189	Sp 4 E	38.0	34.5	3.47
189	Sp 5 A	38.0	34.5	3.46
189	Sp 9 A	38.7	34.5	4.16
189	Sp 8 E	39.5	34.5	5.01
189	Sp 10 E	38.0	34.5	3.51
189	Sp 11 A	36.7	34.5	2.19
189	Sp 13 A	38.4	34.5	3.85
189	Sp 14 E	38.3	34.5	3.75
197	Sp 4 E	28.5	25.3	3.17
197	Sp 5 A	30.0	25.3	4.72
197	Sp 9 A	28.7	25.3	3.40
197	Sp 8 E	29.2	25.3	3.91
207	Sp 1 E	40.0	36.3	3.65
207	Sp 2 A	38.6	36.3	2.31
207	Sp 13 A	39.4	36.3	3.07
216	Sp 4 E	38.0	35.5	2.45
216	Sp 5 A	40.2	35.5	4.63
216	Sp 9 A	37.4	35.5	1.86
216	Sp 8 E	37.3	35.5	1.73
224	Sp 1 E	35.1	31.5	3.58
224	Sp 2 A	34.0	31.5	2.46
224	Sp 13 A	32.9	31.5	1.40
231	Sp 4 E	31.6	29.5	2.08
231	Sp 5 A	32.6	29.5	3.14
231	Sp 9 A	31.3	29.5	1.81
231	Sp 8 E	31.1	29.5	1.65
231	Sp 10 E	31.8	29.5	2.27
231	Sp 11 A	30.9	29.5	1.43
238	Sp 4 E	27.2	25.1	2.06
238	Sp 5 A	27.7	25.1	2.55
238	Sp 9 A	26.8	25.1	1.71
238	Sp 8 E	26.4	25.1	1.24
238	Sp 10 E	27.6	25.1	2.53
238	Sp 11 A	26.2	25.1	1.12

MIDDAY TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
243	Sp 4 E	29.5	26.4	3.12
243	Sp 5 A	29.8	26.4	3.44
243	Sp 9 A	29.0	26.4	2.62
243	Sp 8 E	28.7	26.4	2.29
243	Sp 10 E	30.0	26.4	3.62
243	Sp 11 A	28.4	26.4	2.00
254	Sp 4 E	33.8	30.2	3.66
254	Sp 5 A	34.4	30.2	4.19
258	Sp 4 E	34.5	30.9	3.66
258	Sp 5 A	35.4	30.9	4.53
258	Sp 8 E	33.7	30.9	2.87
258	Sp 10 E	35.0	30.9	4.15
269	Sp 1 E	29.5	24.2	5.35
269	Sp 2 A	28.5	24.2	4.35
269	Sp 9 A	27.9	24.2	3.75
269	Sp 8 E	27.9	24.2	3.72
281	Sp 4 E	20.6	16.3	4.24
281	Sp 5 A	21.8	16.3	5.52
281	Sp 10 E	21.0	16.3	4.70
281	Sp 11 A	20.0	16.3	3.66
286	Sp 4 E	20.5	16.2	4.34
286	Sp 5 A	22.2	16.2	5.96
286	Sp 10 E	21.2	16.2	4.99
286	Sp 11 A	20.0	16.2	3.78
293	Sp 1 E	22.8	19.4	3.38
293	Sp 2 A	22.1	19.4	2.71
293	Sp 9 A	22.1	19.4	2.69
293	Sp 8 E	22.4	19.4	3.05
297	Sp 1 E	25.2	20.3	4.86
297	Sp 2 A	23.3	20.3	3.05
297	Sp 9 A	23.5	20.3	3.17
297	Sp 8 E	24.5	20.3	4.15
307	Sp 1 E	27.6	23.2	4.36
307	Sp 2 A	26.4	23.2	3.15
307	Sp 9 A	26.5	23.2	3.28
307	Sp 8 E	27.2	23.2	3.92

Table 1.3 (cont)

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
148	Sp 10 E	25.1	22.2	2.92
148	Sp 11 A	25.3	22.2	3.12
158	Sp 10 E	25.7	23.0	2.70
158	Sp 11 A	24.4	23.0	1.46
185	Sp 1 E	28.8	26.7	2.06
185	Sp 2 A	28.6	26.7	1.93
185	Sp 4 E	28.7	26.7	1.98
185	Sp 5 A	28.9	26.7	2.19
185	Sp 9 A	28.9	26.7	2.17
185	Sp 8 E	28.8	26.7	2.15
185	Sp 10 E	28.4	26.7	1.74
185	Sp 13 A	28.8	26.7	2.15
189	Sp 1 E	32.1	29.0	3.14
189	Sp 2 A	31.6	29.0	2.60
189	Sp 4 E	31.7	29.0	2.71
189	Sp 5 A	31.8	29.0	2.81
189	Sp 9 A	31.9	29.0	2.90
189	Sp 8 E	32.1	29.0	3.15
189	Sp 10 E	31.6	29.0	2.59
189	Sp 11 A	31.1	29.0	2.07
189	Sp 13 A	31.8	29.0	2.80
189	Sp 14 E	31.9	29.0	2.88
197	Sp 4 E	23.0	20.6	2.43
197	Sp 5 A	23.5	20.6	2.93
197	Sp 9 A	22.9	20.6	2.28
197	Sp 8 E	23.1	20.6	2.52
207	Sp 1 E	30.7	28.2	2.50
207	Sp 2 A	30.2	28.2	2.07
207	Sp 13 A	30.4	28.2	2.26
216	Sp 4 E	30.8	28.4	2.34
216	Sp 5 A	31.5	28.4	3.07
216	Sp 9 A	30.5	28.4	2.06
216	Sp 8 E	30.3	28.4	1.89
224	Sp 1 E	26.3	23.8	2.52
224	Sp 2 A	25.9	23.8	2.04
224	Sp 13 A	25.5	23.8	1.66
231	Sp 4 E	25.9	23.6	2.25
231	Sp 5 A	26.2	23.6	2.59
231	Sp 9 A	25.8	23.6	2.15
231	Sp 8 E	25.6	23.6	2.02
231	Sp 10 E	25.9	23.6	2.29
231	Sp 11 A	25.7	23.6	2.06
238	Sp 4 E	21.6	19.4	2.24
238	Sp 5 A	21.7	19.4	2.31
238	Sp 9 A	21.6	19.4	2.18
238	Sp 8 E	21.2	19.4	1.77
238	Sp 10 E	21.6	19.4	2.18
238	Sp 11 A	21.3	19.4	1.89

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
243	Sp 4 E	23.1	20.6	2.48
243	Sp 5 A	23.2	20.6	2.59
243	Sp 9 A	22.9	20.6	2.37
243	Sp 8 E	22.7	20.6	2.07
243	Sp 10 E	23.1	20.6	2.55
243	Sp 11 A	22.7	20.6	2.16
254	Sp 4 E	25.9	23.4	2.50
254	Sp 5 A	26.1	23.4	2.68
258	Sp 4 E	26.0	23.3	2.69
258	Sp 5 A	26.4	23.3	3.03
258	Sp 8 E	25.4	23.3	2.03
258	Sp 10 E	26.2	23.3	2.89
269	Sp 1 E	17.6	14.1	3.47
269	Sp 2 A	17.4	14.1	3.26
269	Sp 9 A	17.1	14.1	3.02
269	Sp 8 E	17.0	14.1	2.89
281	Sp 4 E	11.5	9.1	2.47
281	Sp 5 A	12.0	9.1	2.90
281	Sp 10 E	11.8	9.1	2.74
281	Sp 11 A	11.6	9.1	2.52
286	Sp 4 E	10.0	7.3	2.69
286	Sp 5 A	10.5	7.3	3.23
286	Sp 10 E	10.3	7.3	2.99
286	Sp 11 A	9.9	7.3	2.67
293	Sp 1 E	15.7	13.2	2.54
293	Sp 2 A	15.5	13.2	2.34
293	Sp 9 A	15.6	13.2	2.41
293	Sp 8 E	15.5	13.2	2.36
297	Sp 1 E	14.1	11.4	2.71
297	Sp 2 A	13.7	11.4	2.24
297	Sp 9 A	13.8	11.4	2.38
297	Sp 8 E	14.1	11.4	2.65
307	Sp 1 E	14.3	11.3	3.04
307	Sp 2 A	14.0	11.3	2.70
307	Sp 9 A	14.0	11.3	2.74
307	Sp 8 E	14.1	11.3	2.77

TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
145	Sp 10 E	24.2	21.8	2.31
145	Sp 11 A	24.3	21.8	2.50
153	Sp 10 E	34.4	33.7	0.69
153	Sp 11 A	36.0	33.7	2.33
161	Sp 10 E	29.4	28.2	1.12
161	Sp 11 A	26.4	28.2	-1.82
170	Sp 10 E	35.9	35.3	0.62
170	Sp 11 A	32.5	35.3	-2.81
192	Sp 1 E	38.2	34.9	3.28
192	Sp 2 A	36.8	34.9	1.85
192	Sp 4 E	37.4	34.9	2.48
192	Sp 5 A	37.2	34.9	2.25
192	Sp 9 A	37.8	34.9	2.82
192	Sp 8 E	38.7	34.9	3.76
192	Sp 10 E	37.7	34.9	2.77
192	Sp 11 A	36.5	34.9	1.57
192	Sp 13 A	37.4	34.9	2.48
192	Sp 14 E	37.9	34.9	2.98
200	Sp 1 E	37.7	35.0	2.78
200	Sp 2 A	37.2	35.0	2.23
200	Sp 10 E	38.0	35.0	3.01
200	Sp 11 A	36.6	35.0	1.67
200	Sp 13 A	37.6	35.0	2.67
207	Sp 4 E	38.2	36.3	1.87
207	Sp 5 A	39.9	36.3	3.59
207	Sp 9 A	37.4	36.3	1.10
207	Sp 8 E	37.3	36.3	1.00
207	Sp 10 E	38.6	36.3	2.29
207	Sp 11 A	37.0	36.3	0.67
216	Sp 1 E	37.6	35.5	2.07
216	Sp 2 A	36.2	35.5	0.62
216	Sp 10 E	36.8	35.5	1.23
216	Sp 11 A	34.7	35.5	-0.81
216	Sp 13 A	35.8	35.5	0.28
222	Sp 1 E	31.9	30.6	1.30
222	Sp 2 A	31.3	30.6	0.75
222	Sp 4 E	31.2	30.6	0.58
222	Sp 5 A	32.4	30.6	1.87
222	Sp 9 A	31.1	30.6	0.53
222	Sp 8 E	31.3	30.6	0.76
222	Sp 10 E	31.9	30.6	1.31
222	Sp 11 A	30.8	30.6	0.18
222	Sp 13 A	31.7	30.6	1.16
229	Sp 4 E	37.1	35.4	1.65
229	Sp 5 A	39.9	35.4	4.51
229	Sp 9 A	36.8	35.4	1.32
229	Sp 8 E	37.4	35.4	1.92
229	Sp 10 E	37.8	35.4	2.35

Table 1.3 (cont)

TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
229	Sp 11 A	35.7	35.4	0.23
240	Sp 1 E	29.2	27.6	1.59
240	Sp 2 A	28.4	27.6	0.80
240	Sp 10 E	30.6	27.6	3.03
240	Sp 11 A	28.8	27.6	1.23
245	Sp 1 E	32.7	28.7	4.05
245	Sp 2 A	31.1	28.7	2.44
245	Sp 5 A	33.5	28.7	4.84
245	Sp 9 A	30.7	28.7	1.99
245	Sp 8 E	30.8	28.7	2.11
245	Sp 10 E	31.5	28.7	2.85
245	Sp 11 A	30.1	28.7	1.43
252	Sp 1 E	33.7	30.4	3.26
252	Sp 2 A	32.4	30.4	1.95
252	Sp 4 E	32.3	30.4	1.92
252	Sp 5 A	32.7	30.4	2.34
252	Sp 9 A	32.1	30.4	1.68
252	Sp 8 E	32.7	30.4	2.34
252	Sp 10 E	33.3	30.4	2.86
252	Sp 11 A	31.7	30.4	1.33
258	Sp 1 E	34.3	30.9	3.42
258	Sp 2 A	32.6	30.9	1.73
258	Sp 9 A	32.4	30.9	1.53
258	Sp 8 E	33.7	30.9	2.87
258	Sp 10 E	35.0	30.9	4.15
258	Sp 11 A	33.0	30.9	2.14
269	Sp 4 E	26.5	24.2	2.31
269	Sp 5 A	26.7	24.2	2.47
269	Sp 10 E	27.6	24.2	3.44
269	Sp 11 A	25.6	24.2	1.42
275	Sp 1 E	13.8	10.9	2.83
275	Sp 2 A	13.0	10.9	2.07
275	Sp 4 E	13.4	10.9	2.44
275	Sp 5 A	13.2	10.9	2.29
275	Sp 9 A	13.2	10.9	2.22
275	Sp 8 E	13.0	10.9	2.08
275	Sp 10 E	13.5	10.9	2.60
275	Sp 11 A	12.7	10.9	1.79
282	Sp 1 E	20.4	17.0	3.42
282	Sp 2 A	17.9	17.0	0.89
282	Sp 9 A	19.0	17.0	2.05
282	Sp 8 E	18.4	17.0	1.46
282	Sp 10 E	21.7	17.0	4.73
282	Sp 11 A	20.4	17.0	3.46
288	Sp 1 E	23.6	19.9	3.70
288	Sp 2 A	20.7	19.9	0.82
288	Sp 4 E	21.5	19.9	1.58
288	Sp 5 A	21.9	19.9	2.02
288	Sp 9 A	21.8	19.9	1.96
288	Sp 8 E	21.3	19.9	1.40
288	Sp 10 E	22.1	19.9	2.24
288	Sp 11 A	20.6	19.9	0.71
295	Sp 4 E	17.1	14.7	2.47
295	Sp 5 A	18.7	14.7	4.04
295	Sp 10 E	18.2	14.7	3.51
295	Sp 11 A	17.3	14.7	2.63
302	Sp 1 E	20.7	16.9	3.89
302	Sp 2 A	18.3	16.9	1.43
302	Sp 4 E	19.2	16.9	2.34
302	Sp 5 A	19.3	16.9	2.46
302	Sp 9 A	19.2	16.9	2.38
302	Sp 8 E	18.6	16.9	1.79
302	Sp 10 E	20.2	16.9	3.33
302	Sp 11 A	19.3	16.9	2.41
309	Sp 4 E	23.2	21.0	2.28
309	Sp 5 A	23.2	21.0	2.23
309	Sp 10 E	24.0	21.0	3.04
309	Sp 11 A	22.6	21.0	1.67
318	Sp 1 E	22.9	19.4	3.47
318	Sp 2 A	20.6	19.4	1.13
318	Sp 4 E	21.2	19.4	1.75
318	Sp 5 A	21.9	19.4	2.42
318	Sp 9 A	21.4	19.4	1.99
318	Sp 8 E	21.6	19.4	2.11
318	Sp 10 E	22.6	19.4	3.14
318	Sp 11 A	21.3	19.4	1.87

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
145	Sp 10 E	19.1	17.6	1.46
145	Sp 11 A	19.0	17.6	1.37
153	Sp 10 E	28.8	26.7	2.13
153	Sp 11 A	29.1	26.7	2.40
161	Sp 10 E	21.5	19.7	1.82
161	Sp 11 A	20.3	19.7	0.62
170	Sp 10 E	26.5	24.8	1.68
170	Sp 11 A	25.3	24.8	0.42
192	Sp 1 E	32.2	29.5	2.74
192	Sp 2 A	31.2	29.5	1.69
192	Sp 4 E	32.0	29.5	2.46
192	Sp 5 A	31.9	29.5	2.41
192	Sp 9 A	32.0	29.5	2.45
192	Sp 8 E	32.0	29.5	2.53
192	Sp 10 E	32.1	29.5	2.57
192	Sp 11 A	31.3	29.5	1.78
192	Sp 13 A	31.0	29.5	1.45
192	Sp 14 E	32.2	29.5	2.71
200	Sp 1 E	28.1	25.6	2.50
200	Sp 2 A	27.8	25.6	2.27
200	Sp 10 E	28.0	25.6	2.47
200	Sp 11 A	27.5	25.6	1.94
200	Sp 13 A	27.8	25.6	2.25
207	Sp 4 E	29.6	28.2	1.47
207	Sp 5 A	30.2	28.2	1.99
207	Sp 9 A	29.5	28.2	1.35
207	Sp 8 E	29.4	28.2	1.26
207	Sp 10 E	29.9	28.2	1.77
207	Sp 11 A	29.4	28.2	1.21
216	Sp 1 E	30.3	28.4	1.88
216	Sp 2 A	29.7	28.4	1.26
216	Sp 10 E	30.1	28.4	1.66
216	Sp 11 A	29.2	28.4	0.75
216	Sp 13 A	29.5	28.4	1.12
222	Sp 1 E	29.6	28.4	1.24
222	Sp 2 A	29.2	28.4	0.81
222	Sp 4 E	29.3	28.4	0.90
222	Sp 5 A	29.8	28.4	1.38
222	Sp 9 A	29.2	28.4	0.83
222	Sp 8 E	29.0	28.4	0.65
222	Sp 10 E	29.7	28.4	1.27
222	Sp 11 A	28.8	28.4	0.45
222	Sp 13 A	29.5	28.4	1.11
229	Sp 4 E	29.7	27.6	2.05
229	Sp 5 A	30.7	27.6	3.08
229	Sp 9 A	29.5	27.6	1.82
229	Sp 8 E	29.6	27.6	1.94
229	Sp 10 E	29.8	27.6	2.19

Table 1.3 (cont)

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
SPARTINA OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
229	Sp 11 A	29.1	27.6	1.42
240	Sp 1 E	24.2	22.8	1.47
240	Sp 2 A	23.8	22.8	1.06
240	Sp 10 E	24.6	22.8	1.82
240	Sp 11 A	24.3	22.8	1.51
245	Sp 1 E	21.5	18.8	2.67
245	Sp 2 A	21.0	18.8	2.17
245	Sp 5 A	22.1	18.8	3.32
245	Sp 9 A	20.8	18.8	1.98
245	Sp 8 E	20.8	18.8	2.01
245	Sp 10 E	21.2	18.8	2.40
245	Sp 11 A	20.6	18.8	1.82
252	Sp 1 E	26.1	24.1	1.98
252	Sp 2 A	25.6	24.1	1.55
252	Sp 4 E	25.6	24.1	1.54
252	Sp 5 A	25.7	24.1	1.60
252	Sp 9 A	25.6	24.1	1.51
252	Sp 8 E	25.9	24.1	1.79
252	Sp 10 E	26.1	24.1	2.02
252	Sp 11 A	25.5	24.1	1.40
258	Sp 1 E	25.6	23.3	2.23
258	Sp 2 A	24.9	23.3	1.59
258	Sp 9 A	24.9	23.3	1.53
258	Sp 8 E	25.4	23.3	2.03
258	Sp 10 E	26.2	23.3	2.89
258	Sp 11 A	25.4	23.3	2.07
269	Sp 4 E	16.6	14.1	2.50
269	Sp 5 A	16.4	14.1	2.31
269	Sp 10 E	16.9	14.1	2.81
269	Sp 11 A	16.1	14.1	2.03
275	Sp 1 E	15.7	13.2	2.53
275	Sp 2 A	15.1	13.2	1.89
275	Sp 4 E	15.5	13.2	2.27
275	Sp 5 A	15.3	13.2	2.13
275	Sp 9 A	15.3	13.2	2.13
275	Sp 8 E	15.1	13.2	1.87
275	Sp 10 E	15.7	13.2	2.51
275	Sp 11 A	15.1	13.2	1.84
282	Sp 1 E	10.7	8.6	2.07
282	Sp 2 A	9.9	8.6	1.28
282	Sp 9 A	10.4	8.6	1.81
282	Sp 8 E	10.2	8.6	1.52
282	Sp 10 E	11.5	8.6	2.88
282	Sp 11 A	11.1	8.6	2.51
288	Sp 1 E	10.6	8.4	2.17
288	Sp 2 A	9.6	8.4	1.17
288	Sp 4 E	10.2	8.4	1.73
288	Sp 5 A	10.1	8.4	1.67
288	Sp 9 A	10.2	8.4	1.78
288	Sp 8 E	10.4	8.4	1.96
288	Sp 10 E	10.6	8.4	2.11
288	Sp 11 A	9.9	8.4	1.49
295	Sp 4 E	7.6	5.4	2.19
295	Sp 5 A	8.1	5.4	2.64
295	Sp 10 E	8.0	5.4	2.59
295	Sp 11 A	7.9	5.4	2.47
302	Sp 1 E	8.4	5.6	2.79
302	Sp 2 A	7.6	5.6	1.93
302	Sp 4 E	8.1	5.6	2.47
302	Sp 5 A	8.0	5.6	2.33
302	Sp 9 A	8.0	5.6	2.37
302	Sp 8 E	7.6	5.6	2.00
302	Sp 10 E	8.2	5.6	2.57
302	Sp 11 A	8.0	5.6	2.34
309	Sp 4 E	14.5	12.7	1.77
309	Sp 5 A	14.3	12.7	1.56
309	Sp 10 E	14.6	12.7	1.87
309	Sp 11 A	14.3	12.7	1.59
318	Sp 1 E	7.6	5.1	2.49
318	Sp 2 A	6.9	5.1	1.75
318	Sp 4 E	7.2	5.1	2.09
318	Sp 5 A	7.2	5.1	2.07
318	Sp 9 A	7.3	5.1	2.13
318	Sp 8 E	7.2	5.1	2.02
318	Sp 10 E	7.6	5.1	2.47
318	Sp 11 A	7.2	5.1	2.06

Table 1.4. Seasonal course of temperatures inside (Ti) and outside (To) open and closed top chambers in the Scirpus community. Data are mean values for entire 24 hr periods or during four hours of midday (10:00-14:00).

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
SCIRPUS OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
157	Sc 1 E	22.0	20.0	1.97
157	Sc 2 A	21.9	20.0	1.95
169	Sc 1 E	25.4	23.8	1.61
169	Sc 2 A	25.4	23.8	1.62
182	Sc 1 E	28.0	26.3	1.72
182	Sc 2 A	27.6	26.3	1.25
189	Sc 1 E	31.1	29.5	1.63
189	Sc 2 A	30.8	29.5	1.32
197	Sc 1 E	22.6	20.8	1.86
197	Sc 2 A	21.7	20.8	0.97
202	Sc 1 E	32.3	30.0	2.27
202	Sc 2 A	32.1	30.0	2.07
215	Sc 1 E	31.0	29.3	1.67
215	Sc 2 A	30.4	29.3	1.05
224	Sc 1 E	26.4	23.7	2.69
224	Sc 2 A	25.6	23.7	1.85
229	Sc 1 E	30.8	27.8	2.97
229	Sc 2 A	30.0	27.8	2.17
237	Sc 1 E	20.2	17.7	2.52
237	Sc 2 A	19.7	17.7	1.99
244	Sc 1 E	23.6	20.8	2.86
244	Sc 2 A	22.8	20.8	2.03
256	Sc 1 E	24.1	23.2	0.90
256	Sc 2 A	23.9	23.2	0.70
261	Sc 1 E	26.9	24.3	2.55
261	Sc 2 A	26.7	24.3	2.35
267	Sc 1 E	19.5	17.0	2.54
267	Sc 2 A	19.0	17.0	1.99
272	Sc 1 E	22.2	18.8	3.41
272	Sc 2 A	20.7	18.8	1.88
281	Sc 1 E	11.5	8.7	2.77
281	Sc 2 A	10.9	8.7	2.24
288	Sc 1 E	11.5	8.3	3.21
288	Sc 2 A	10.8	8.3	2.47
307	Sc 1 E	11.7	11.3	0.39
307	Sc 2 A	13.5	11.3	2.24
312	Sc 1 E	12.9	12.7	0.25
312	Sc 2 A	14.3	12.7	1.59

MIDDAY TEMPERATURE DIFFERENCES (Ti - To) 1987
SCIRPUS OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
145	Sc 1 E	23.3	22.8	0.45
145	Sc 2 A	22.4	22.8	-0.38
157	Sc 1 E	30.9	29.5	1.40
157	Sc 2 A	31.8	29.5	2.24
169	Sc 1 E	33.6	33.3	0.27
169	Sc 2 A	34.6	33.3	1.27
182	Sc 1 E	36.2	34.0	2.23
182	Sc 2 A	34.5	34.0	0.58
189	Sc 1 E	37.3	35.4	1.88
189	Sc 2 A	37.7	35.4	2.27
197	Sc 1 E	27.4	25.6	1.81
197	Sc 2 A	26.4	25.6	0.80
202	Sc 1 E	41.3	38.4	2.85
202	Sc 2 A	42.1	38.4	3.72
215	Sc 1 E	36.6	34.8	1.82
215	Sc 2 A	35.9	34.8	1.05
224	Sc 1 E	36.6	31.1	5.48
224	Sc 2 A	33.9	31.1	2.71
229	Sc 1 E	40.7	35.4	5.30
229	Sc 2 A	38.9	35.4	3.42
237	Sc 1 E	27.0	23.4	3.59
237	Sc 2 A	25.5	23.4	2.10
244	Sc 1 E	32.1	27.1	5.04
244	Sc 2 A	29.9	27.1	2.81
256	Sc 1 E	27.3	25.8	1.45
256	Sc 2 A	26.8	25.8	0.98
261	Sc 1 E	33.0	28.6	4.35
261	Sc 2 A	32.2	28.6	3.62
267	Sc 1 E	30.4	25.8	4.63
267	Sc 2 A	29.0	25.8	3.19
272	Sc 1 E	35.0	28.4	6.67
272	Sc 2 A	31.8	28.4	3.47
281	Sc 1 E	20.9	16.1	4.82
281	Sc 2 A	21.0	16.1	4.84
288	Sc 1 E	25.4	19.6	5.81
288	Sc 2 A	25.0	19.6	5.41
307	Sc 1 E	23.4	23.7	-0.29
307	Sc 2 A	26.6	23.7	2.84
312	Sc 1 E	21.6	22.2	-0.65
312	Sc 2 A	24.5	22.2	2.30

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
SCIRPUS CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
147	Sc 1 E	21.6	20.1	1.54
147	Sc 2 A	21.2	20.1	1.08
153	Sc 1 E	27.5	25.1	2.42
153	Sc 2 A	27.1	25.1	2.01
180	Sc 1 E	27.2	23.6	3.61
180	Sc 2 A	25.8	23.6	2.26
204	Sc 1 E	32.0	28.8	3.24
204	Sc 2 A	31.4	28.8	2.61
220	Sc 1 E	30.0	26.7	3.33
220	Sc 2 A	28.8	26.7	2.17
275	Sc 1 E	17.4	13.2	4.22
275	Sc 2 A	17.5	13.2	4.26
293	Sc 1 E	16.1	13.3	2.77
293	Sc 2 A	15.9	13.3	2.62
299	Sc 1 E	4.6	4.2	0.38
299	Sc 2 A	6.8	4.2	2.60

MIDDAY TEMPERATURE DIFFERENCES (Ti - To) 1987
SCIRPUS CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
147	Sc 1 E	23.6	22.1	1.48
147	Sc 2 A	22.7	22.1	0.61
153	Sc 1 E	35.3	32.3	2.98
153	Sc 2 A	34.7	32.3	2.36
180	Sc 1 E	37.5	33.0	4.42
180	Sc 2 A	34.5	33.0	1.46
204	Sc 1 E	41.1	37.6	3.55
204	Sc 2 A	41.7	37.6	4.08
220	Sc 1 E	38.0	32.2	5.79
220	Sc 2 A	35.4	32.2	3.24
275	Sc 1 E	32.1	23.2	8.94
275	Sc 2 A	33.3	23.2	10.16
293	Sc 1 E	23.9	19.9	4.02
293	Sc 2 A	24.1	19.9	4.21
299	Sc 1 E	16.8	17.0	-0.22
299	Sc 2 A	19.6	17.0	2.66

Table 1.5. Seasonal course of temperatures inside (Ti) and outside (To) open and closed top chambers in the Mixed community. Data are mean values for entire 24 hr periods or during four hours of midday (10:00-14:00).

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
MIXED OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
157	Mx 11 E	22.0	20.3	1.69
157	Mx 12 A	21.6	20.3	1.31
169	Mx 11 E	26.1	24.4	1.78
169	Mx 12 A	24.8	24.4	0.45
182	Mx 11 E	28.1	26.7	1.42
182	Mx 12 A	26.9	26.7	0.14
189	Mx 11 E	31.2	29.5	1.70
189	Mx 12 A	30.0	29.5	0.48
197	Mx 11 E	22.3	20.8	1.50
197	Mx 12 A	21.8	20.8	0.95
202	Mx 11 E	32.0	29.8	2.15
202	Mx 12 A	31.1	29.8	1.28
215	Mx 11 E	30.7	29.2	1.57
215	Mx 12 A	29.7	29.2	0.55
224	Mx 11 E	25.5	24.0	1.57
224	Mx 12 A	24.6	24.0	0.62
229	Mx 11 E	29.8	27.8	2.00
229	Mx 12 A	29.1	27.8	1.23
237	Mx 11 E	19.4	17.7	1.73
237	Mx 12 A	19.3	17.7	1.66
244	Mx 11 E	22.6	20.8	1.87
244	Mx 12 A	22.1	20.8	1.29
256	Mx 11 E	23.7	23.2	0.50
256	Mx 12 A	23.5	23.2	0.23
261	Mx 11 E	27.2	24.6	2.66
261	Mx 12 A	26.7	24.6	2.08
267	Mx 11 E	19.4	17.1	2.33
267	Mx 12 A	18.8	17.1	1.73
272	Mx 11 E	21.0	18.7	2.32
272	Mx 12 A	20.4	18.7	1.73
279	Mx 11 E	16.7	14.6	2.14
279	Mx 12 A	16.0	14.6	1.39
288	Mx 11 E	10.5	8.5	1.99
288	Mx 12 A	9.8	8.5	1.30
307	Mx 11 E	13.7	11.4	2.25
307	Mx 12 A	13.7	11.4	2.29
312	Mx 11 E	14.5	12.8	1.67
312	Mx 12 A	14.3	12.8	1.49

24 HOUR TEMPERATURE DIFFERENCES (Ti - To) 1987
MIXED CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
147	Mx 11 E	21.8	19.8	2.06
147	Mx 12 A	21.7	19.8	1.89
166	Mx 11 E	30.6	29.0	1.59
166	Mx 12 A	29.6	29.0	0.63
192	Mx 11 E	32.6	30.1	2.51
192	Mx 12 A	32.1	30.1	1.95
210	Mx 11 E	26.5	23.6	2.98
210	Mx 12 A	25.8	23.6	2.26
249	Mx 11 E	23.1	21.4	1.69
249	Mx 12 A	23.1	21.4	1.67
261	Mx 11 E	26.4	23.9	2.48
261	Mx 12 A	26.0	23.9	2.08
281	Mx 11 E	12.2	9.0	3.14
281	Mx 12 A	11.5	9.0	2.45
293	Mx 11 E	15.6	13.2	2.39
293	Mx 12 A	15.5	13.2	2.34

MIDDAY TEMPERATURE DIFFERENCES (Ti - To) 1987
MIXED OPEN-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
145	Mx 11 E	24.1	21.7	2.34
145	Mx 12 A	22.6	21.7	0.88
157	Mx 11 E	31.8	30.2	1.62
157	Mx 12 A	29.7	30.2	-0.46
169	Mx 11 E	36.1	34.1	1.94
169	Mx 12 A	32.0	34.1	-2.15
182	Mx 11 E	36.0	34.4	1.56
182	Mx 12 A	33.3	34.4	-1.12
189	Mx 11 E	37.7	36.0	1.69
189	Mx 12 A	34.8	36.0	-1.17
197	Mx 11 E	26.9	25.9	0.96
197	Mx 12 A	25.8	25.9	-0.07
202	Mx 11 E	40.7	37.9	2.81
202	Mx 12 A	38.5	37.9	0.54
215	Mx 11 E	36.7	35.0	1.70
215	Mx 12 A	34.3	35.0	-0.77
224	Mx 11 E	33.4	31.9	1.53
224	Mx 12 A	30.8	31.9	-1.07
229	Mx 11 E	38.3	35.7	2.63
229	Mx 12 A	35.7	35.7	0.00
237	Mx 11 E	24.8	23.4	1.31
237	Mx 12 A	24.2	23.4	0.72
244	Mx 11 E	29.2	27.4	1.79
244	Mx 12 A	27.7	27.4	0.33
256	Mx 11 E	26.4	26.0	0.41
256	Mx 12 A	26.0	26.0	-0.06
261	Mx 11 E	33.3	29.7	3.56
261	Mx 12 A	31.8	29.7	2.09
267	Mx 11 E	28.9	26.6	2.23
267	Mx 12 A	27.0	26.6	0.40
272	Mx 11 E	31.0	28.7	2.23
272	Mx 12 A	29.2	28.7	0.43
279	Mx 11 E	26.7	23.0	3.65
279	Mx 12 A	23.5	23.0	0.45
288	Mx 11 E	23.4	20.7	2.62
288	Mx 12 A	20.2	20.7	-0.51
307	Mx 11 E	27.1	23.9	3.15
307	Mx 12 A	27.4	23.9	3.49
312	Mx 11 E	24.5	22.2	2.32
312	Mx 12 A	24.5	22.2	2.31

MIDDAY TEMPERATURE DIFFERENCES (IN - OUT) 1987
MIXED CLOSED-TOP

JULIAN DATE	CHAMBER	Ti	To	Ti-To
147	Mx 11 E	24.4	21.5	2.93
147	Mx 12 A	23.9	21.5	2.40
166	Mx 11 E	41.0	39.9	1.17
166	Mx 12 A	37.3	39.9	-2.56
192	Mx 11 E	39.1	35.9	3.21
192	Mx 12 A	37.0	35.9	1.08
210	Mx 11 E	36.2	32.4	3.78
210	Mx 12 A	33.6	32.4	1.24
249	Mx 11 E	23.4	21.8	1.55
249	Mx 12 A	23.4	21.8	1.53
261	Mx 11 E	33.3	29.7	3.56
261	Mx 12 A	31.8	29.7	2.09
281	Mx 11 E	23.4	17.1	6.33
281	Mx 12 A	20.1	17.1	3.00
293	Mx 11 E	22.8	19.5	3.32
293	Mx 12 A	22.0	19.5	2.45

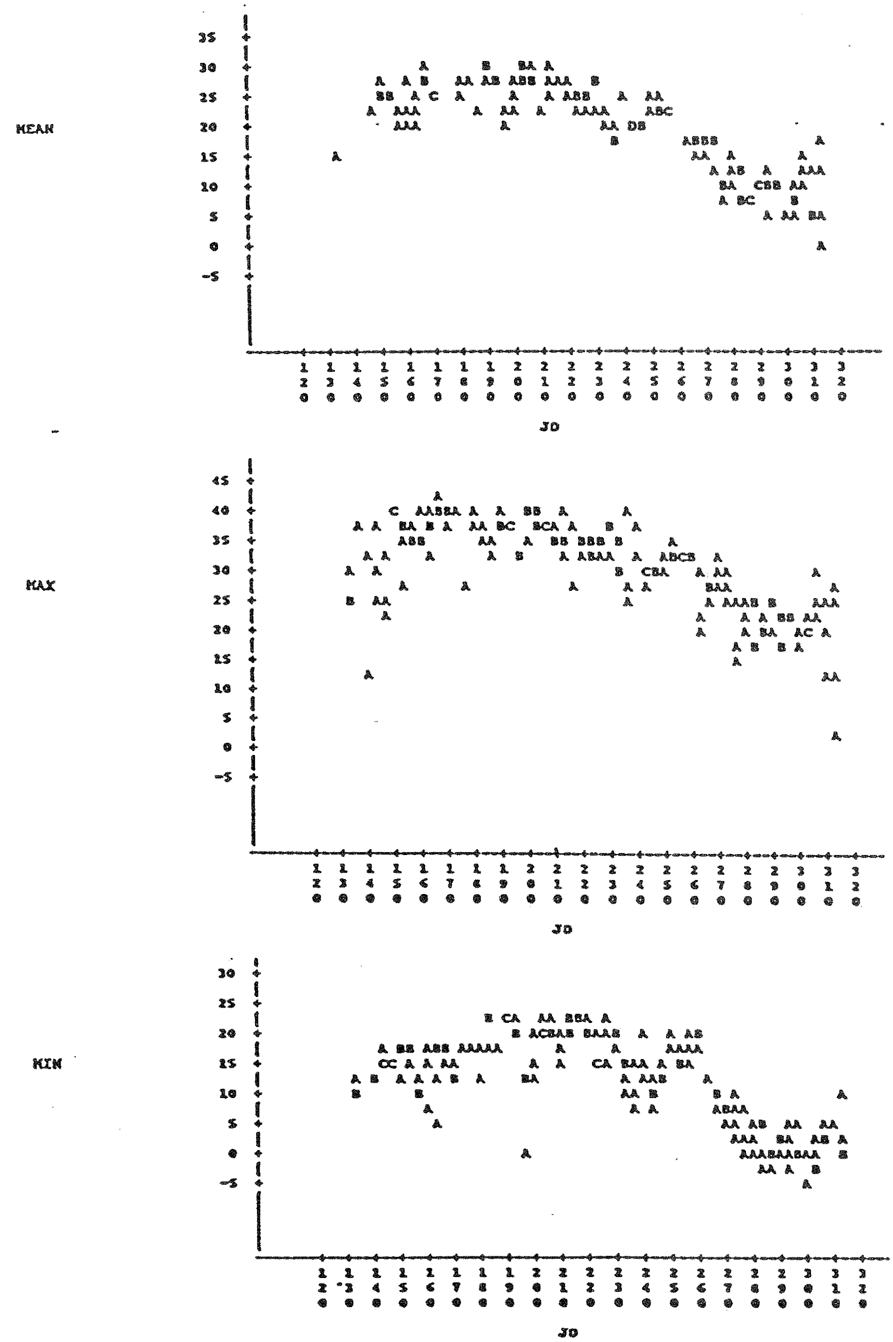


Figure 1.9. Seasonal course of mean, maximum, and minimum ambient temperatures. Data values are averages from two thermocouples in each community placed at canopy height.

Table 1.6. Air temperature differences (T_i - T_o, C) in open and closed top chambers from the three marsh communities. Temperatures were averaged between 10:00 and 14:00 (Midday) and 0:00 and 24:00 (24 hr). Mean $\pm$ S.D. (N).

	Spartina	Mixed	Scirpus
		OPEN TOP	
24 - Hr	1.9 $\pm$ 0.4 (124)$^{+}$	1.5 $\pm$ 0.6 (38)	1.9 $\pm$ 0.7 (38)
Midday	2.1 $\pm$ 1.2 (124)	1.2 $\pm$ 1.4 (38)	2.7 $\pm$ 1.9 (38)
		CLOSED TOP	
24 - Hr	2.5 $\pm$ 0.4 (84)	2.1 $\pm$ 0.6 (16)	2.6 $\pm$ 1.1 (16)
Midday	3.3 $\pm$ 1.1 (84)	2.3 $\pm$ 1.8 (16)	3.7 $\pm$ 2.7 (16)

$^{+}$ each observation is the average of all measurements on one day for a single chamber.

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 $T_i - T_o$ (Fig 1.10A,B). In the Scirpus community, differences between air $T_i - T_o$ and vegetation $T_i - T_o$ of 1-4 C were recorded (Fig 1.10C). The average midday vegetation $T_i - T_o$ for 3 days in June 1987 was ca. 1.5 C (Table 1.7).

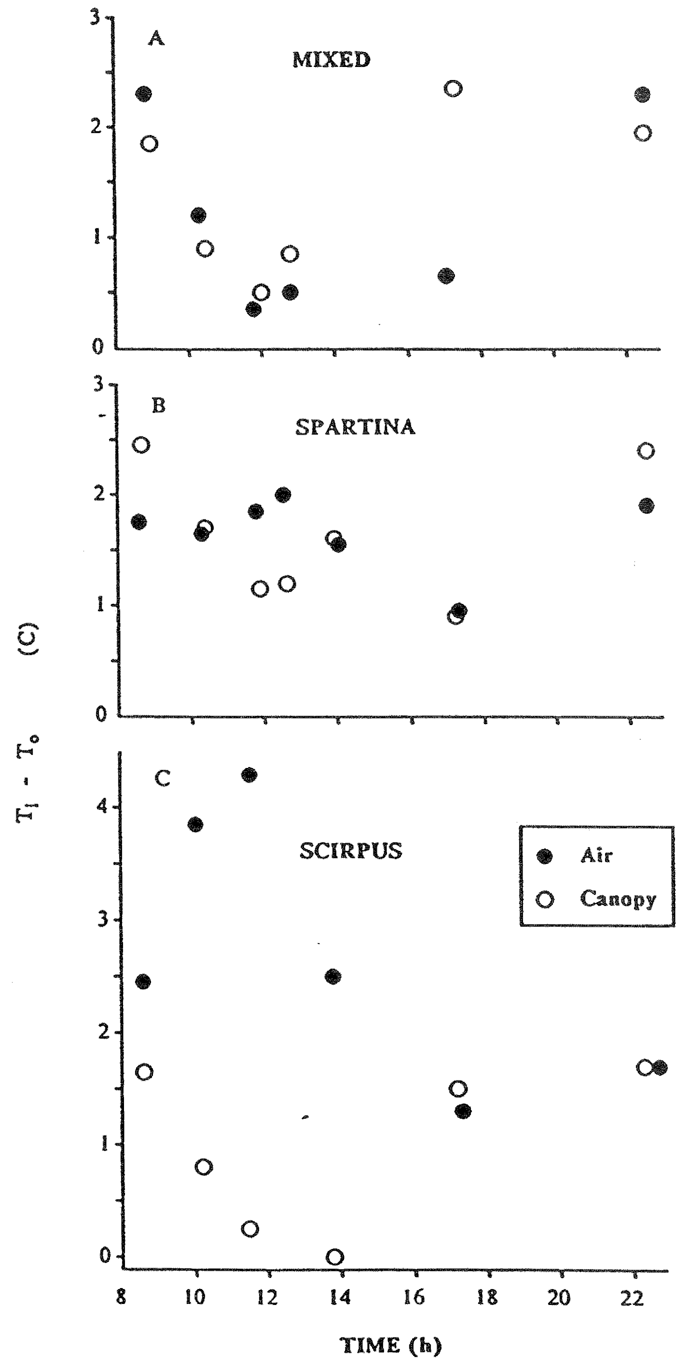


Figure 1.10. Temperature differences during the day inside to outside an open top chamber, $T_i - T_o$, in the Mixed (A), Spartina (B), and Scirpus (C) communities. Air temperatures (●) were recorded with shielded thermocouples and vegetation temperatures (○) with a hand held infra-red thermometer.

Table 1.7. Midday vegetation : air temperature differences measured with a hand held infra-red thermometer.

Date	Community	$[CO_2]$	Top	T_i-T_o	N
6/16	Mixed	Elevated	Both	2.26	5
		Ambient	Both	1.34	5
		Both	Closed	2.10	6
		Both	Open	1.35	4
6/18	All	Elevated	Both	1.77	7
		Ambient	Both	1.70	5
		Both	Closed	3.25	2
		Both	Open	1.44	10
6/19	Mixed	Elevated	Open	2.73	3
		Ambient	Open	1.40	3
	Spartina	Elevated	Open	-.45	2
		Ambient	Open	0.0	2
	Mx & Sp	Both	Closed	2.42	4
		Both	Open	1.15	10

CHAPTER 2

PLANT GROWTH, PRIMARY PRODUCTIVITY AND SENESCENCE

A central goal of our research has been to determine the effect of elevated CO_2 on growth processes in these high marsh communities. Since CO_2 may affect plant growth at all stages of the life cycle we have used serial censuses of shoot number and size, taken throughout the season, as our primary data base. We report here the results of a single season of exposure to elevated CO_2. Because the study species are perennial plants, reproducing vegetatively from belowground rhizomes, continuing exposure to elevated CO_2 for several years will be necessary before generalizations can be made with confidence.

Materials and Methods

Vegetation Sampling

Plant growth in each plot was followed by serial, non-destructive censuses of shoot number, shoot weight and aboveground biomass. Sampling methods were designed to minimize destructive changes to the plant canopy while providing sufficient material and demographic information to describe treatment responses. Approximately five days were required to census one community. Net primary productivity (NPP) was calculated using the method of Smalley (1959) for *Spartina* and *Distichlis*, and cumulative mortality for *Scirpus* (Hopkinson et al. 1980). All other measures of aboveground biomass, shoot numbers and shoot weight are for green tissue only.

Scirpus

Aboveground biomass of *Scirpus* consists solely of erect photosynthetic shoots. *Scirpus* was censused in each plot by measuring each shoot to the nearest 1 cm. Regression equations relating shoot height to shoot biomass were calculated from destructive harvests of shoots outside of the experimental plots. Aboveground biomass per plot was calculated as the sum of estimated individual shoot dry weights. Separate regressions were calculated for the SCIRPUS and MIXED communities at each census. All harvested shoots were dried at 60 C and weighed.

Three to five shoots were also harvested from within each plot at each census, measured, and compared to the confidence limits of the regression equations. This comparison showed that the allometric relationship between shoot length and dry weight was not affected by treatment so single equations were sufficient to estimate shoot dry weights for all plots in a community. Shoots harvested within plots were also used for calculating specific leaf weights (SLW = g cm^{-2}). Leaf area, ie. green shoot area, was estimated by measuring the base width, apex width, and height of one rhomboidal face of each shoot.

Spartina and Distichlis

Because of the high density of Spartina and Distichlis shoots, shoot number, biomass, and leaf area were estimated by sub-sampling each plot. Each plot in the SPARTINA and MIXED communities was divided into permanent 100 cm^2 quadrats using monofilament nylon line. Five quadrats per plot were randomly selected for sub-sampling at the beginning of the season. Combined, these five quadrats represented 10% of the total plot area. All shoots were counted within each quadrat at each census.

Shoot density per plot was estimated by extrapolation from the mean density in the 5 quadrats. Shoot biomass and leaf area were estimated from limited destructive harvests in each plot at each census. All living shoots within three 25 cm^2 areas located

2 cm from quadrats in each plot were harvested. Typically, 25-40 stems were collected per plot per census. Senescent material was measured separately from green tissue and no area within a plot was harvested more than once during the season. Leaf area was measured with an electronic leaf area meter. Mean dry weight per shoot was multiplied by shoot density to estimate aboveground biomass per plot.

At peak standing biomass (late August) the area sub-sampled within each plot was expanded to 10 quadrats (20% of the plot area) and 80-100 shoots harvested. Estimates of shoot density and dry weight were compared using both the original and expanded methods. There were no significant differences between methods for within treatment estimates of growth (mean of five plots, t-test).

<u>Belowground Growth</u>

Belowground growth was estimated by the recovery and analysis of regrowth cores (Gallagher et al. 1984). During the winter of 1986, two 5 cm x 30 cm cores were taken at random from three replicates of each treatment in each community (= 54 cores). The cored locations were then repacked with a peat:vermiculite mixture (2:1 dry volume) wetted with river water. These locations were recored in November 1987 and the regrowth cores extracted. The cores were washed clean of peat and vermiculite and all roots and rhizomes separated, dried, and weighed.

<u>Plant Growth Analysis</u>

The relative increases in aboveground biomass (Biomass RGR), shoot number (Shoot Density RGR) and shoot dry weight (Shoot Weight RGR) were calculated after the methods of Hunt (1982). Cubic polynomials were fit to the ln transformed data (Y) from each census for each plot by least squares regression. First derivatives were evaluated at the date of census.

$$RGR = d(\ln Y)/dx = 1/Y\ dy/dx.$$

Derivatives were not evaluated at the ends of the fitted curves (first and last censuses).

Statistical Analysis

Treatment means within a census were analysed by analysis of variance (ANOVA) based on five replicates per treatment arranged in a randomized block design. Variance estimates for aboveground biomass, shoot density, and shoot weight were based on among plot variance only. Pairwise comparison of means was by least significant difference (*a priori* comparisons: ELEVATED vs AMBIENT, AMBIENT vs CONTROL) or minimum significant difference (*a posteriori* comparisons) (Sokal and Rohlf 1981). Percentages were arc-sin transformed before analysis by ANOVA.

Relative growth rates were compared using Friedman's method for randomized blocks (Sokal and Rohlf 1981). This non-parametric test uses the ranking of variates within blocks and therefore does not require the estimation of variance components. For significant treatment effects to be inferred, the ranking of variates must be identical within all five blocks.

Results

Shoot Density

Shoots density of *Scirpus* was higher in plots with elevated CO_2 in both SCIRPUS and MIXED communities (Fig 2.1A, 2.1B). In both cases the effects of CO_2 first became significant at peak density in August and extended through the end of the season.

There was also a significant difference between shoot densities of Scirpus from AMBIENT and CONTROL plots in the SCIRPUS community (Fig 2.1A). This chamber effect was not, however, found in the MIXED community (Fig 2.1B).

The relative rate of change in shoot density (Shoot Density RGR) was consistently higher in SCIRPUS community ELEVATED plots than AMBIENT plots but this difference was only significant in July, immediately preceding peak densities (Fig 2.2A). In the MIXED community, the effect of CO_2 on Scirpus Shoot Density RGR was seen later in the season, with significant differences between ELEVATED and AMBIENT plots in August and September (Fig 2.2B). These results indicate both a greater relative allocation of carbon into new shoots and a slower senescence of existing shoots under elevated CO_2.

Shoot densities showed a much more gradual increase over time in the SPARTINA (Fig 2.2C) and MIXED-C_4 communities (Fig 2.3A). Shoot emergence occurred slightly earlier than in Scirpus, with a large number of shoots appearing in mid to late April. There were no significant differences in shoot densities or Shoot Density RGR (data not shown) among ELEVATED, AMBIENT, or CONTROL plots at any time.

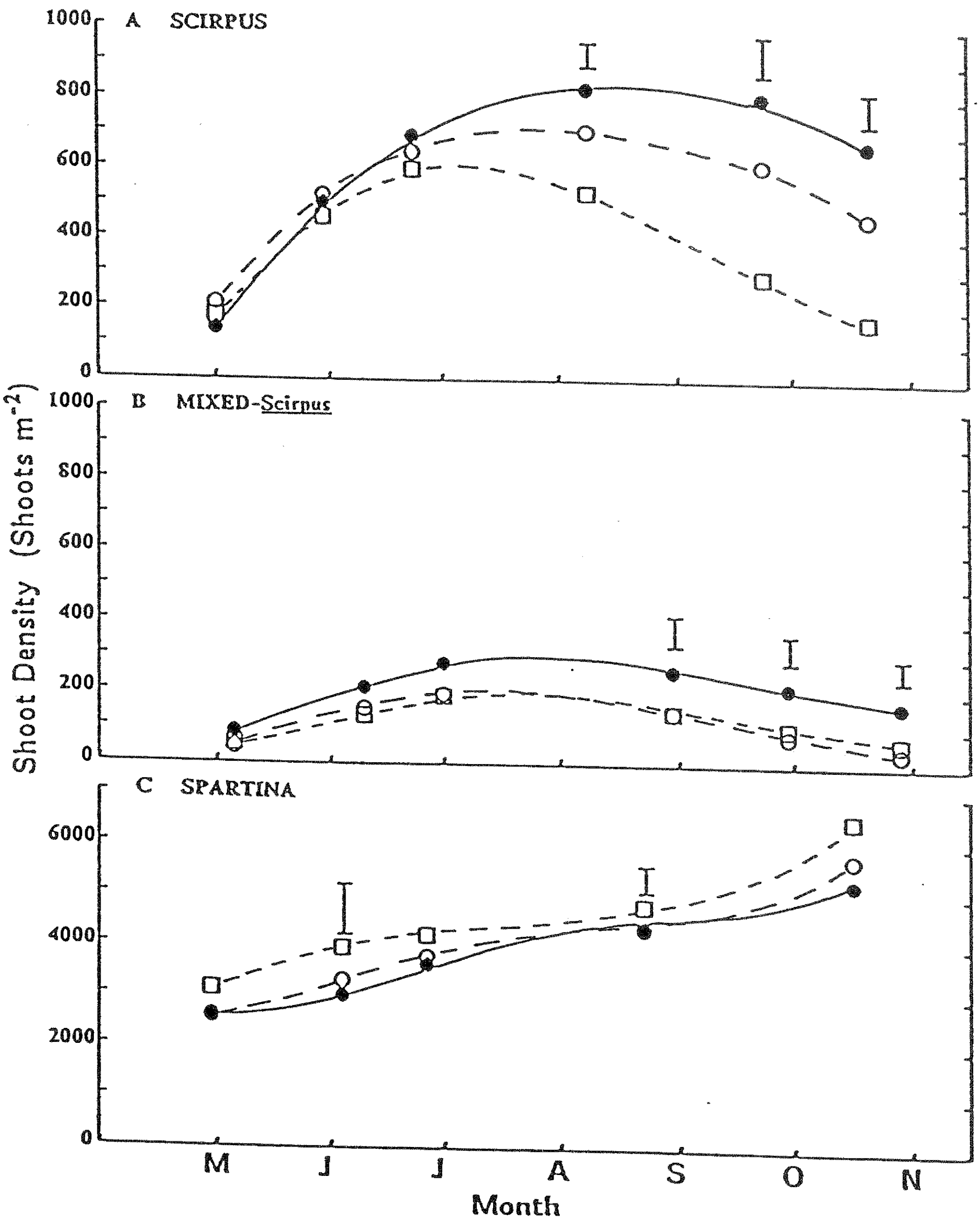


Figure 2.1. The change in shoot density in SCIRPUS (A), MIXED-<u>Scirpus</u> (B), and SPARTINA (C) plots. Treatments were ELEVATED (●), AMBIENT (○), and CONTROL (□). Vertical bars are the LSD (P<.05) and are included where significant differences occur (A and B) or at the second and fourth censuses to indicate variablity (C).

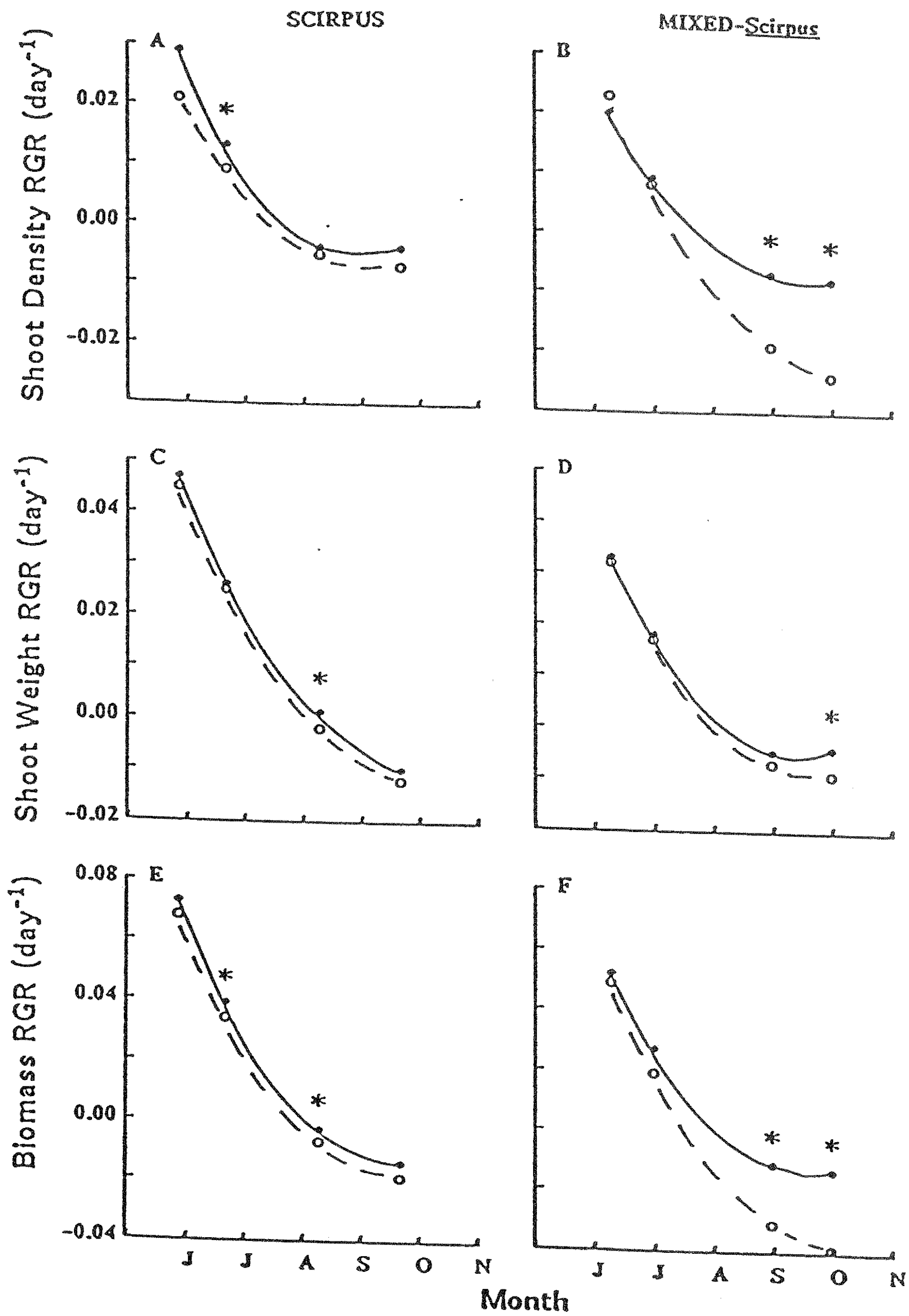


Figure 2.2. Relative change in Shoot Density, Shoot Weight, and Aboveground Biomass from SCIRPUS (A,C,E) and MIXED-Scirpus (B,D,F) plots exposed to ELEVATED (●) or AMBIENT (O) CO_2 treatments. Asterixes denote a significant difference ($P<.05$) between RGR means within a census.

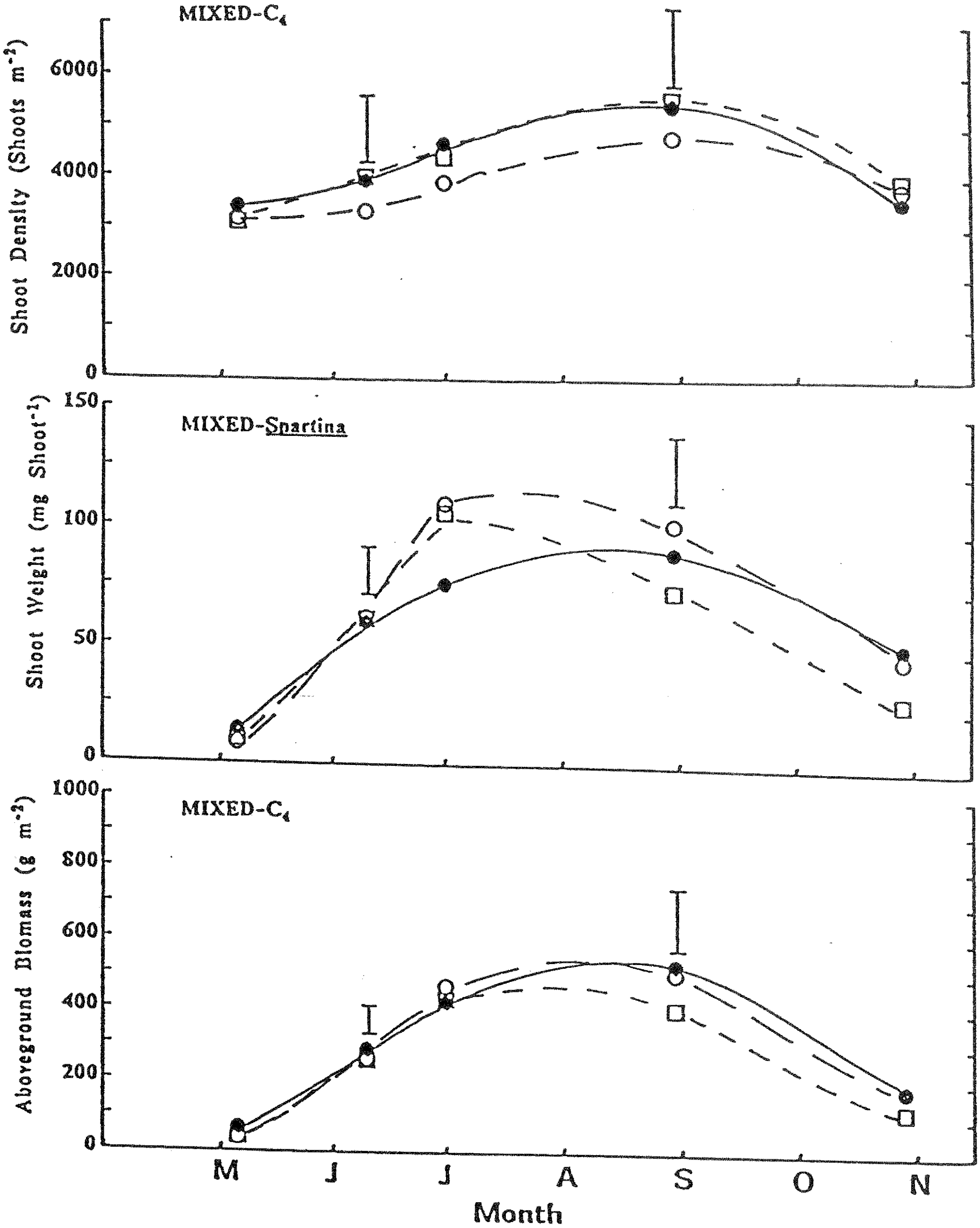


Figure 2.3 The change in shoot density, shoot weight, and aboveground biomass in the Mixed community. Treatments are as in Fig 2.1.

Shoot Weight

CO_2 had no effect on mean shoot weight in the SCIRPUS community (Fig 2.4A). Shoots of <u>Scirpus</u> in the MIXED community were less than 50% of the size of shoots in the SCIRPUS community and there was a significant increase in shoot weight due to CO_2 beginning in late August and extending through the end of the season (Fig 2.4B). There was a significant effect of CO_2 on Shoot Weight RGR in the SCIRPUS and Mixed communities in late August and September (Figs 2.2C,2.2D). This response was particularly evident in the MIXED community where shoot weight declined very little through November. There was a significant chamber effect on shoot weight in the SCIRPUS community in September and October and in the MIXED community in late October (Fig 2.4A,B). There were no CO_2 effects on shoot weight in <u>Spartina</u> from the pure (Fig 4C) or Mixed (Fig 2.3B) communities. There were also no effects of CO_2 or chamber on SLW from any of The study species (Table 2.1).

Shoot Height

Green shoot height increased rapidly in <u>Scirpus</u>, with the greatest mean shoot height occurring in August (Table 2.2). There was no significant effect of CO_2 on shoot height in either the SCIRPUS or MIXED communities through the August census. At the final census in October, green <u>Scirpus</u> - Mixed shoots under elevated CO_2 were significantly taller than ambients, reflecting the strong effect of CO_2 on delaying senescence.

Although CO_2 did not change maximum mean shoot height, there was a significant effect on the shoot height distribution in the SCIRPUS community (Fig 2.5). In August, at peak standing biomass, there were ca. 60% more shoots in the 90-120 cm height class under elevated CO_2. There was no CO_2 effect on any other height class at this census.

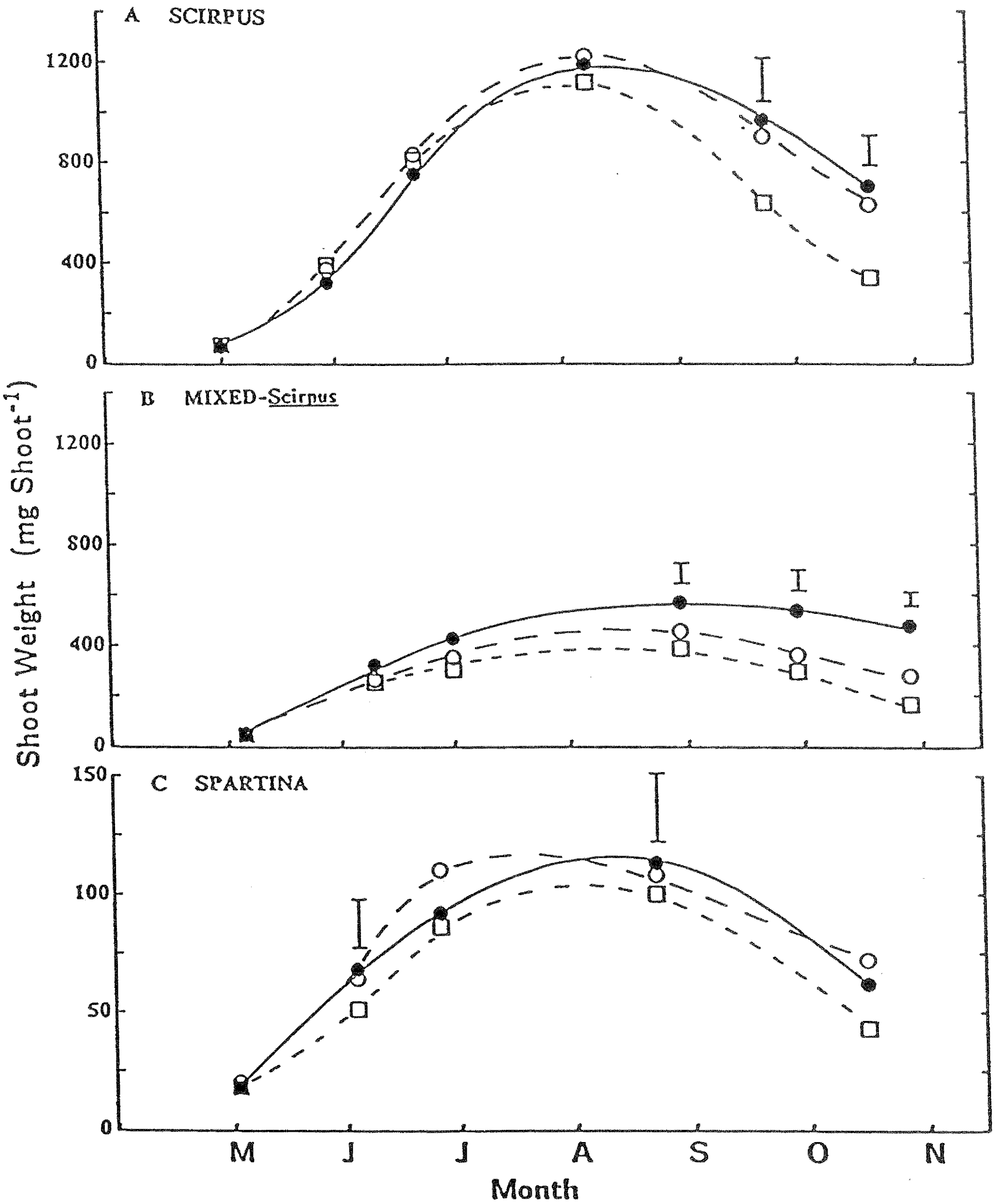


Figure 2.4. The change in shoot weight with time in SCIRPUS (A), MIXED-Scirpus (B), and SPARTINA (C) plots. Treatments are as in Fig. 2.1.

Table 2.1. Specific leaf weights at peak standing biomass from ELEVATED, AMBIENT, AND CONTROL plots in three marsh communities. Mean ± (s.e.).

Community	ELEVATED	AMBIENT	CONTROL
	g/cm^2		
SCIRPUS	.0274 (.0016)	.0260 (.0008)	.0274 (.0004)
MIXED-*Scirpus*	.0288 (.0013)	.0268 (.0013)	.0251 (.0019)
SPARTINA	.0233 (.0036)	.0198 (.0003)	.0217 (.0006)
MIXED-*Spartina*	.0198 (.0010)	.0210 (.0005)	.0204 (.0004)
MIXED-*Distichlis*	.0141 (.0011)	.0142 (.0005)	.0147 (.0006)

Table 2.2. Scirpus stem heights from the SCIRPUS and MIXED communities. Mean ± (s.d.), n=5.

	May	June	July	August	October
			cm		
SCIRPUS					
Elevated	13.6 (1.6)	53.1 (5.8)	83..3 (3.6)	91.0 (4.6)	66.0 (6.8)
Ambient	14.5 (1.9)	57.9 (4.2)	88.4 (9.6)	91.3 (11.9)	60.7 (10.8)
Control	14.7 (2.2)	58.6 (3.2)	87.3 (8.0)	86.9 (9.7)	38.6 (11.3)
MIXED					
Elevated	13.1 (4.7)	59.3 (8.2)	63.8 (8.3)	63.3 (6.0)	55.4 (5.7)
Ambient	11.7 (3.2)	53.2 (6.7)	58.7 (7.9)	53.4 (5.1)	38.3 (3.3)
Control	11.7 (3.5)	51.2 (8.5)	52.9 (10.8)	47.6 (6.2)	28.5 (5.1)

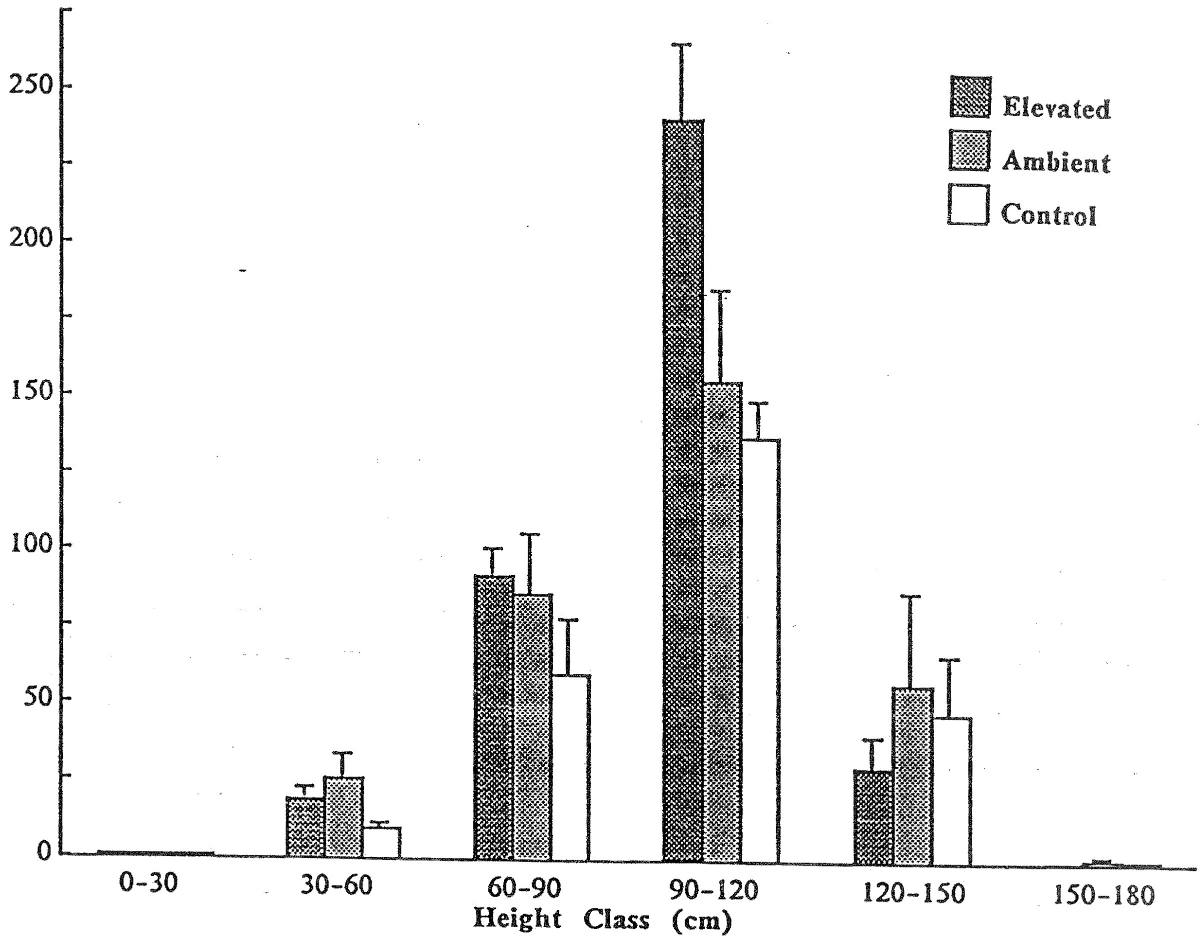


Figure 2.5. Numbers of shoots in different height classes in the Scirpus community at the August census (peak standing biomass). Vertical bars indicate one standard error.

Aboveground Biomass

Aboveground live biomass in the SCIRPUS community increased rapidly between shoot emergence in late-April and the end of July, reaching a maximum of between 600 and 900 g/m^2 in early August (Fig 2.5A). Biomass was significantly higher in ELEVATED plots in September and October. Peak standing biomass in Scirpus from the MIXED community was less than 20% of that from the SCIRPUS community and there was also a significant response to elevated CO_2 (Fig 2.6B). As with shoot density there was a significant chamber effect on aboveground biomass only in the SCIRPUS community.

Although elevated CO_2 had no significant effect on aboveground biomass in the SCIRPUS community until September, there were small but significant increases in Biomass RGR due to CO_2 in both July and August (Fig 2.2E). Scirpus in the MIXED community showed similar, although non-significant, differences in Biomass RGR at these times and much greater differences during September and October (Fig 2.2F). The CO_2 effects on aboveground biomass were therefore due in part to an increase in the efficiency of new growth (principally through new shoot production) and in part to a delay in the loss of dry weight through senescence.

There were no treatment effects on aboveground biomass in Spartina (Fig 2.6C). Shoot emergence began in mid April and peak biomass of about 500 g/m^2 was reached in late August. Peak aboveground biomass in the C_4 component of the MIXED community also showed no effect of CO_2 (Fig 2.3C) and was very similar to the SPARTINA community. Analysis of Dry Weight RGR also showed no treatment effects or consistent trends in either community (data not shown).

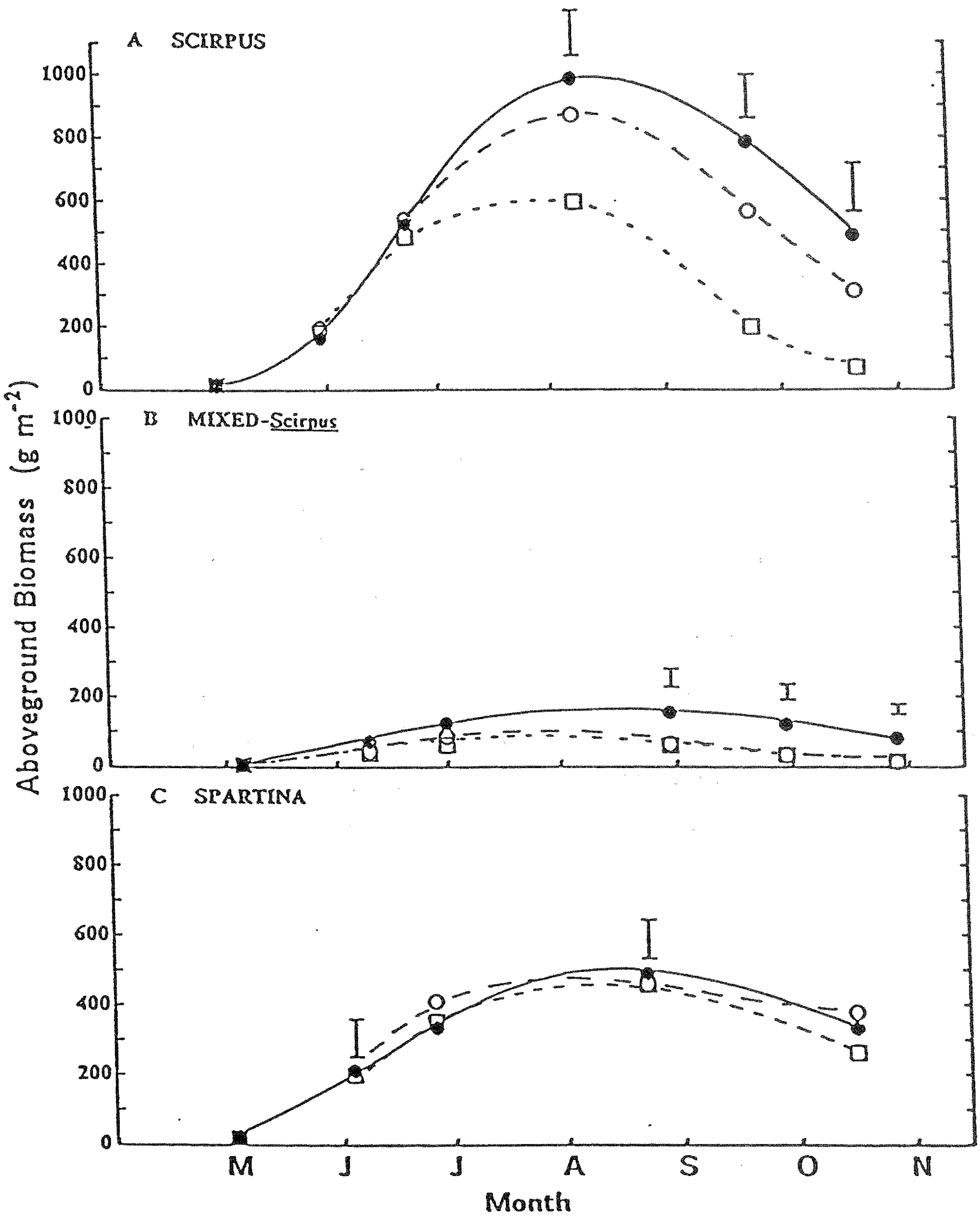


Figure 2.6. The change in aboveground biomass with time in SCIRPUS (A), MIXED-<u>Scirpus</u> (B), and SPARTINA and MIXED-C_4 (C) plots. Treatments are as in Fig. 2.1.

The percentage of total _Scirpus_ biomass present as dead tissue at the final census in November was significantly lower under elevated CO_2 in both the SCIRPUS and MIXED communities (Table 2.3). Again, there was a significant chamber effect in the SCIRPUS but not the MIXED community. Senescence of the two C_4 species appears to have progressed somewhat more rapidly in the MIXED than in the SPARTINA community but there was no effect of CO_2 in either case.

Elevated CO_2 caused a significant increase in aboveground net primary productivity (NPP) in _Scirpus_ from both the SCIRPUS and MIXED communities (Table 2.4). Although peak live biomass in the SCIRPUS community was not significantly higher in ELEVATED plots, sustained growth later in the season led to greater NPP under elevated CO_2. Senescent _Scirpus_ shoots weighed less per cm than did living shoots which resulted in lower NPP than peak aboveground live biomass (Fig 2.6A, 2.6B). Net primary productivity in the C_4 species was greater than in _Scirpus_ but was unaffected by elevated CO_2.

Reproduction in Scirpus

Approximately 80% of all shoots flowered in the SCIRPUS community and from 45% to 60% flowered in the MIXED community (Fig 2.7). The number setting seed was lower: 25% to 40% in the SCIRPUS community and 10% to 30% in the MIXED community. There was no CO_2 effect on sexual reproduction in either community. There was, however, a significant chamber effect present.

Table 2.3. Percentage of total biomass (live + senescent) which was senescent at the final census in November 1987 in ELEVATED, AMBIENT, AND CONTROL plots in three marsh communities. Mean ± (s.e.).

Community	ELEVATED	AMBIENT	CONTROL
		%	
SCIRPUS	35.5 (4.6)[a+]	45.7 (5.6)[b]	79.3 (6.1)[c]
MIXED-*Scirpus*	37.8 (4.6)[a]	80.1 (2.4)[b]	68.7 (6.3)[b]
SPARTINA	45.3 (4.1)[a]	44.9 (6.0)[a]	53.1 (6.5)[a]
MIXED-*Spartina*	51.8 (9.0)[a]	56.3 (6.6)[a]	69.6 (9.6)[a]
MIXED-*Distichlis*	66.7 (9.3)[a]	64.3 (12.7)[a]	57.2 (11.3)[a]

[+] similar superscript denotes no significant difference within a community, $P<.05$, except SCIRPUS ELEVATED vs AMBIENT where $P<.10$.

Table 2.4. Net primary productivity from ELEVATED, AMBIENT, AND CONTROL plots in three marsh communities. Mean ± (s.e.).

Community	ELEVATED	AMBIENT	CONTROL
	g/m^2		
SCIRPUS	539 (47)$^{a+}$	463 (44)^{b}	345 (21)^{c}
MIXED-*Scirpus*	139 (25)^{a}	78 (15)^{b}	63 (11)^{b}
SPARTINA	645 (22)^{a}	668 (61)^{a}	650 (58)^{a}
MIXED-C_4	732 (49)^{a}	694 (47)^{a}	660 (74)^{a}

$^{+}$ similar superscript denotes no significant difference within a community, $P<.05$.

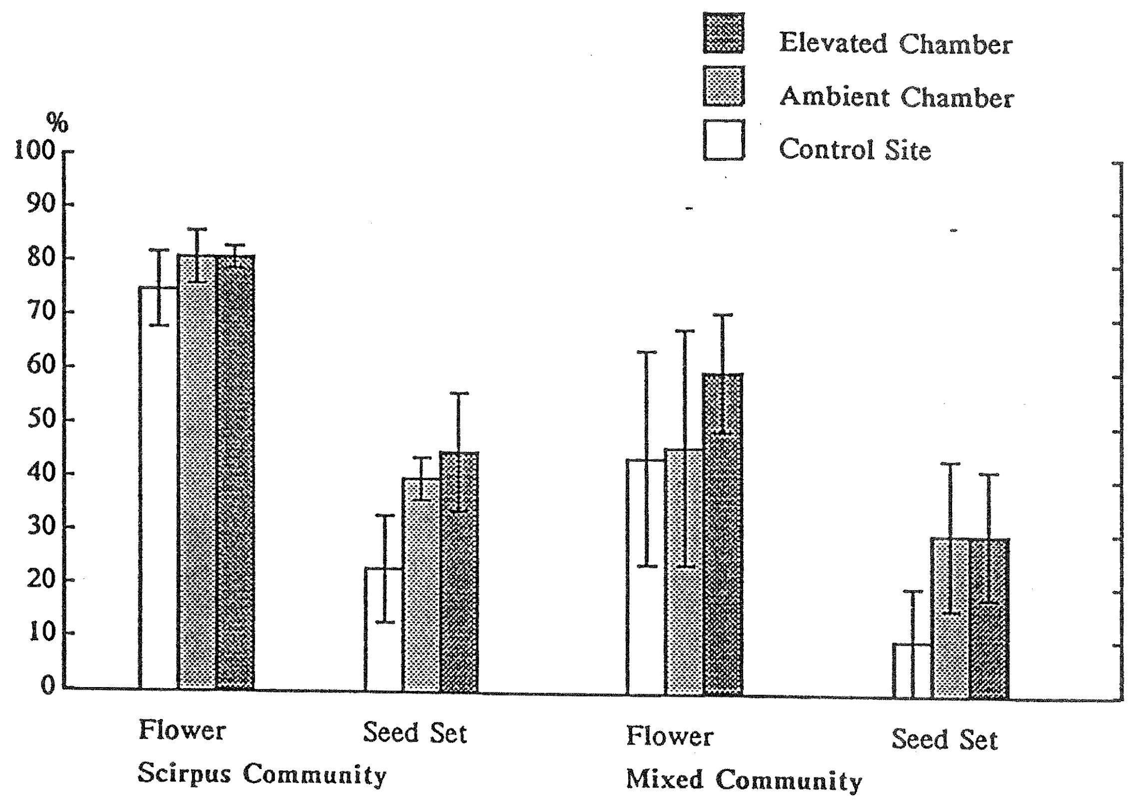


Figure 2.7. The effect of elevated CO_2 on flowering and seed set in Scirpus from pure and Mixed communities.

Belowground Biomass

Results from the regrowth cores showed strong trends towards increasing root growth in Scirpus under elevated CO_2 (Table 2.5). Because of relatively large variation and small sample sizes these trends were not statistically significant. In particular there was poor recovery of rhizomes from Ambient and Control treatments. We have increased our sample size and improved the core packing technique to correct these problems. Recovery of roots and rhizomes was better in Spartina although there was also fairly high variance among samples and no significant differences among treatments.

Table 2.5. Belowground production to a depth of .1m in the SCIRPUS and SPARTINA communities from Elevated, Ambient, and Control plots. Data are from regrowth cores put in place in Jan 1987 and re-cored Nov 1987. Mean ± (s.d.), n = 3.

		$g\ m^{-2}$	
		roots	rhizomes
SCIRPUS			
	Elevated	200 (26)	241 (180)
	Ambient	159 (63)	175 (64)$^{+}$
	Control	137 (23)	28 (--)*
SPARTINA			
	Elevated	162 (28)	107 (29)
	Ambient	119 (40)	144 (87)
	Control	140 (12)	128 (8)

$^{+}$ n = 2, * n = 1.

CHAPTER 3

Single Leaf Photosynthesis and Net Ecosystem CO_2 Exchange

A. The effect of elevated CO_2 on photosynthesis of leaves

Light response curves for single leaf photosynthesis measured in the field on Scirpus olneyi and Spartina patens grown at ambient or elevated CO_2 concentration are shown in Figure 3.1. Two light response curves were made for each leaf tested; one at ambient CO_2 (open circles) and one at elevated CO_2 (680 ppm, closed circles). Square symbols are means with error bars for maximum photosynthesis in 5-8 leaves. Measurements were made between June 29 and August 10, 1987.

The response of photosynthesis to light was clearly different in the two species. In the C_3 sedge, Scirpus olneyi, photosynthesis was higher at all values of PPF above the compensation point when measured at 680 ppm than when measured at normal ambient CO_2 concentration and the same was true in plants grown at normal ambient CO_2. Thus, growing the plants in elevated CO_2 made little difference in their capacity to respond to increased CO_2 (Figure 3.1). On the other hand, photosynthesis in leaves of the C_4 grass, Spartina patens, grown in normal ambient CO_2 was higher in elevated CO_2 than in normal ambient CO_2 concentration but in leaves grown in elevated CO_2, photosynthesis was essentially the same at elevated and normal ambient CO_2 concentration. After 12 weeks of growth in elevated CO_2 concentration, the only significant acclimation of photosynthesis to elevated CO_2 was a slight reduction of photosynthetic capacity of the C_4 species when tested at ambient CO_2 concentration.

Light response curves were generated by fitting a hyperbolic light model to the data with values of photosynthesis the dependent variable and PPF the independent variable. Data were

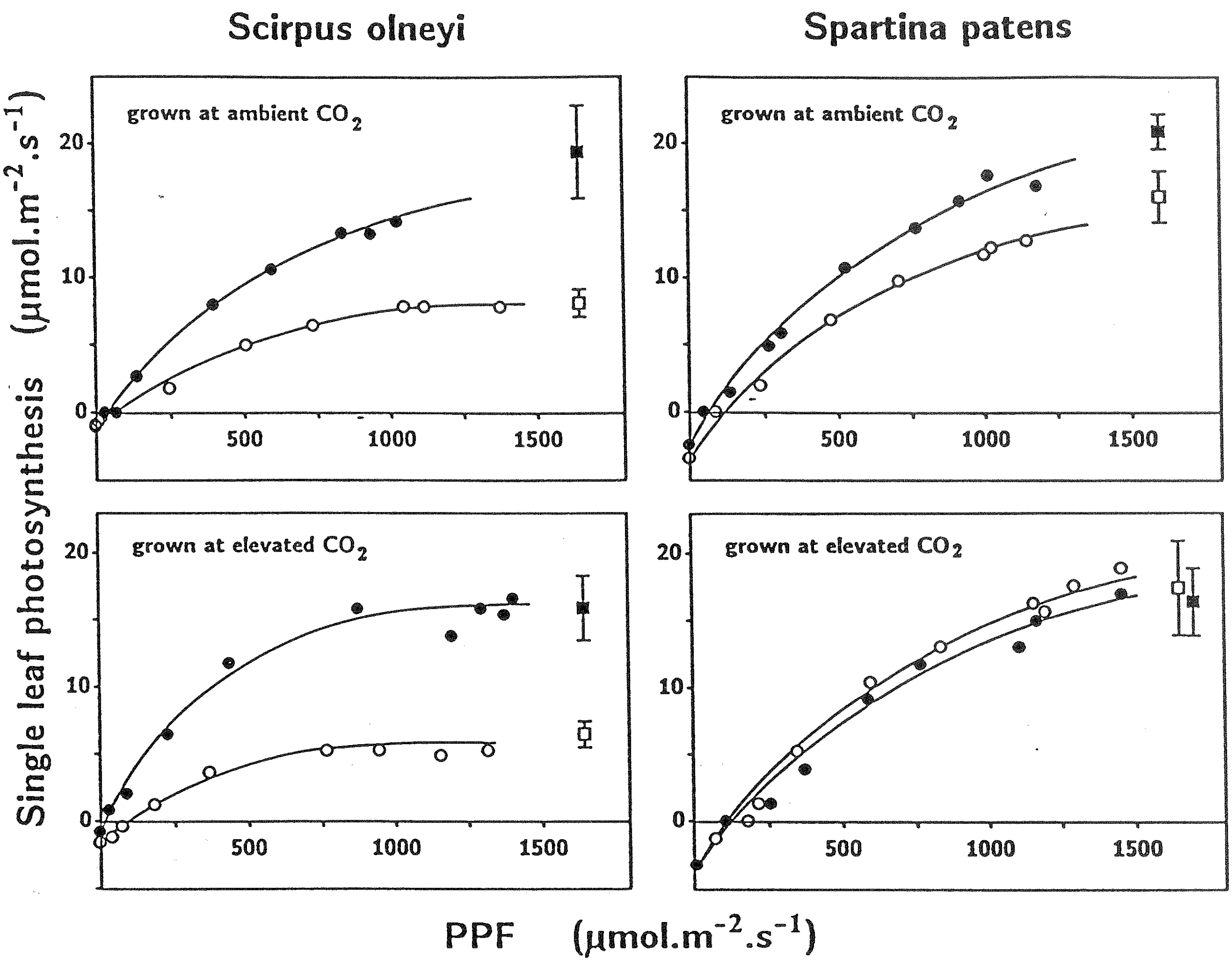


Figure 3.1. Photosynthesis of leaves of plants in situ. Each pair of curves constructed on the same leaf tissue. For Scirpus, this was a single triangular stem and for Spartina this was several leaves in the assimilation chamber simultaneously. The square symbols are means with error bars of 5-8 stems of Scirpus and 30-50 leaves of Spartina.

Table 3.1. The parameters of photosynthesis for single leaves determined from the data on measurements of photosynthesis obtained using the ADC portable infra-red gas analyser and Parkinson leaf chamber. Data on photosynthesis and PPF were fit to a hyperbolic model and the parameters in this table calculated from this model. A/A means that the plant as grown in ambient CO_2 and the data for that line were determined at ambient CO_2.

	A_{max}	Respiration	Initial Slope	Compensation Point
Scirpus A/A	7.94 ± 1.18	-2.40 ± 1.0	0.03 ± .009	99.42 ± 23.2
Scirpus A/E	19.41 ± 3.40	-4.47 ± 2.4	0.06 ± .007	66.58 ± 43.1
Scirpus E/A	6.47 ± 0.93	-1.15 ± 0.2	0.02 ± .002	64.18 ± 12.9
Scirpus E/E	15.89 ± 2.42	-1.49 ± 0.5	0.07 ± .009	22.12 ± 6.5
Spartina A/A	16.11 ± 1.91	-3.99 ± .40	0.03 ± .003	106.80 ± 5.2
Spartina A/E	20.90 ± 1.26	-2.86 ± .13		76.01 ± 8.9
Spartina E/A	17.42 ± 3.45	-8.11 ± 3.2	0.04 ± .006	139.70 ± 23.9
Spartina E/E	16.38 ± 2.48	-3.55 ± .42	0.03 ± .0004	114.17 ± 13.3

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Spartina E/A	17.42 ± 3.45	-8.11 ± 3.2	0.04 ± .006	139.70 ± 23.9
Spartina E/E	16.38 ± 2.48	-3.55 ± .42	0.03 ± .0004	114.17 ± 13.3

taken as described above. These curves were analysed to determine the effect of growth in elevated CO_2 on maximum values (discussed above), dark respiration, the initial slope of the light response curve, and the compensation value. The results of this analysis appear in Table 3.1. Growth in elevated CO_2 reduced respiration rates in both species compared to growth in normal ambient CO_2 although the effect was greater in Scirpus than in Spartina. Testing the effect of elevated CO_2 on respiration of plants grown in normal ambient CO_2 yielded different effects in the two species: Scirpus olneyi had higher respiration rates in elevated CO_2 whether grown or tested in that concentration, but Spartina patens had highest respiration rates in ambient CO_2 whether grown or tested in ambient CO_2 concentration. The initial slope of the light response curve was highest in elevated CO_2 in Scirpus but in Spartina, the effects of elevated CO_2 were inconsistent. The compensation point decreased in elevated CO_2 in both treatments and both species and was lower in Scirpus than in Spartina.

B. The effect of elevated CO_2 on net ecosystem CO_2 exchange.

1. Methods.

In order to determine the effect of elevated CO_2 on ecosystem gas exchange, a top was placed on the open top chamber and the drop in CO_2 concentration across the chamber was determined. Knowing the flow rate through the chamber permitted the calculation of photosynthesis. The gas circuit for determining the drop in [CO_2] across the chamber is shown in Figure 3.2 A. Flow rate through the chamber was determined periodically using a hot wire anemometer to measure air velocity across the exit pipe. Typically, this value was 1100 $\pm$ 25 $l.min^{-1}$ which exchange the chamber volume $\pm$ 2.5 times per minute. The gas analyser was calibrated routinely and the automatic calibration circuit for this is shown in Figure 3.2 B. A trace of

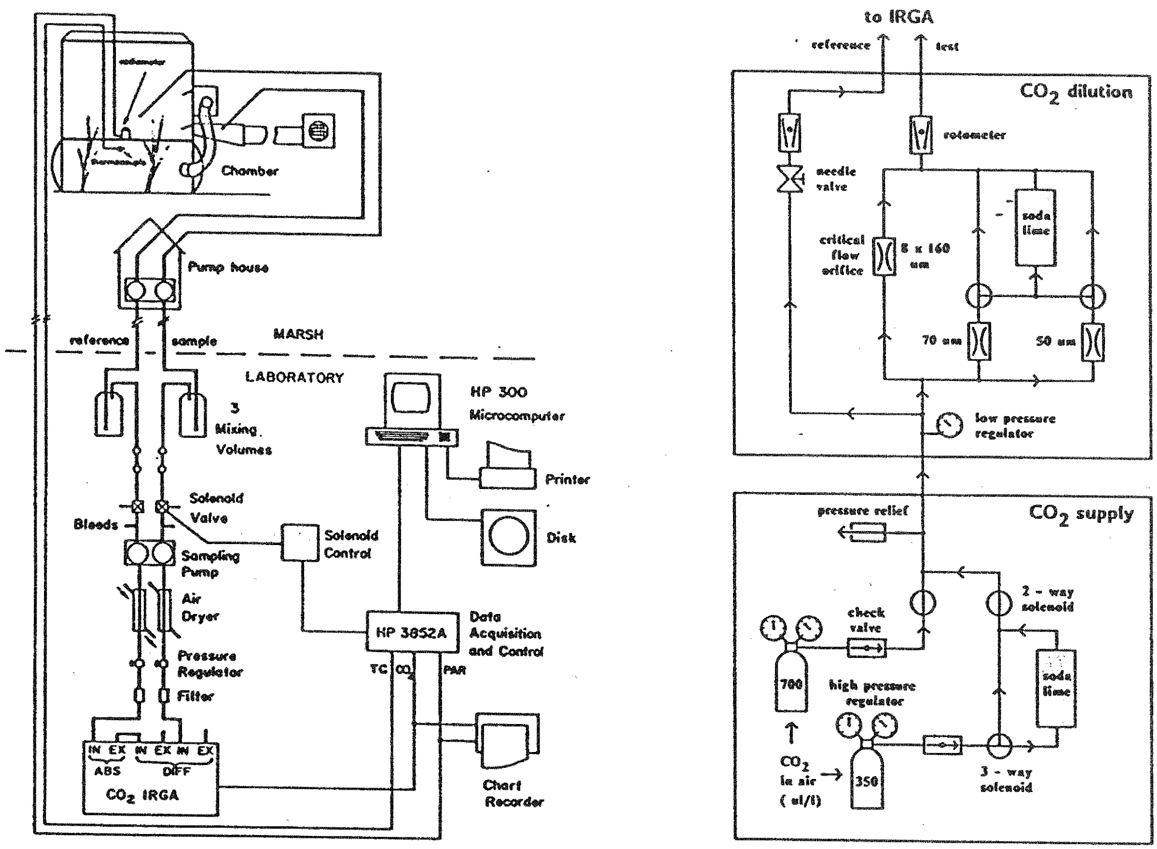

Figure 3.2. Gas circuit for measuring net ecosystem photosynthesis and gas circuit for automated calibration of IRGA.

the net ecosystem CO_2 exchange (NCE) and incident photosynthetically active photon flux (PPF) for one day is shown in Figure 3.3. The data in this figure are evidence that the chamber can be used for measurements of ecosystem gas exchange when the open top is restricted.

2. Effect of elevated CO_2 on NCE

Throughout the growing season, NCE was periodically measured in all chambers in each community simultaneously. This approach was alternated with measurement of combinations of chambers in all three communities measured at the same time so as to see effects of environmental variables across species. The results of one set of measurement for ten chambers in each community are shown in Figure 3.4. The left hand panels are diurnal traces for ecosystem net CO_2 exchange (NCE) and the right hand panels contain the data on PPF and air temperature inside one of the chambers in each community. There is a trace of NCE for elevated CO_2 and one for ambient CO_2 constructed from the mean and 95% confidence interval of the data for five chambers. The frequency of measurement was 10/hr averaged in 15 minute intervals. The days represented are 29 June for Scirpus, 8 July for Spartina, and 11-12 July for Mixed. The effect of elevated CO_2 is clearly evident in the Scirpus community. Traces similar to these were made for data collected throughout the season but, for the sake of brevity, they are not presented here. Instead, the integrated NCE data for each chamber are tabulated along with integrated daily PPF, dry weight, and NCE normalized on dry weight and on PPF in Table 3.2.

3. Interaction of light with the effect of CO_2 on NCE.

In order to determine the effect of elevated CO_2 on the response of NCE to light, the mean of the values for the data for

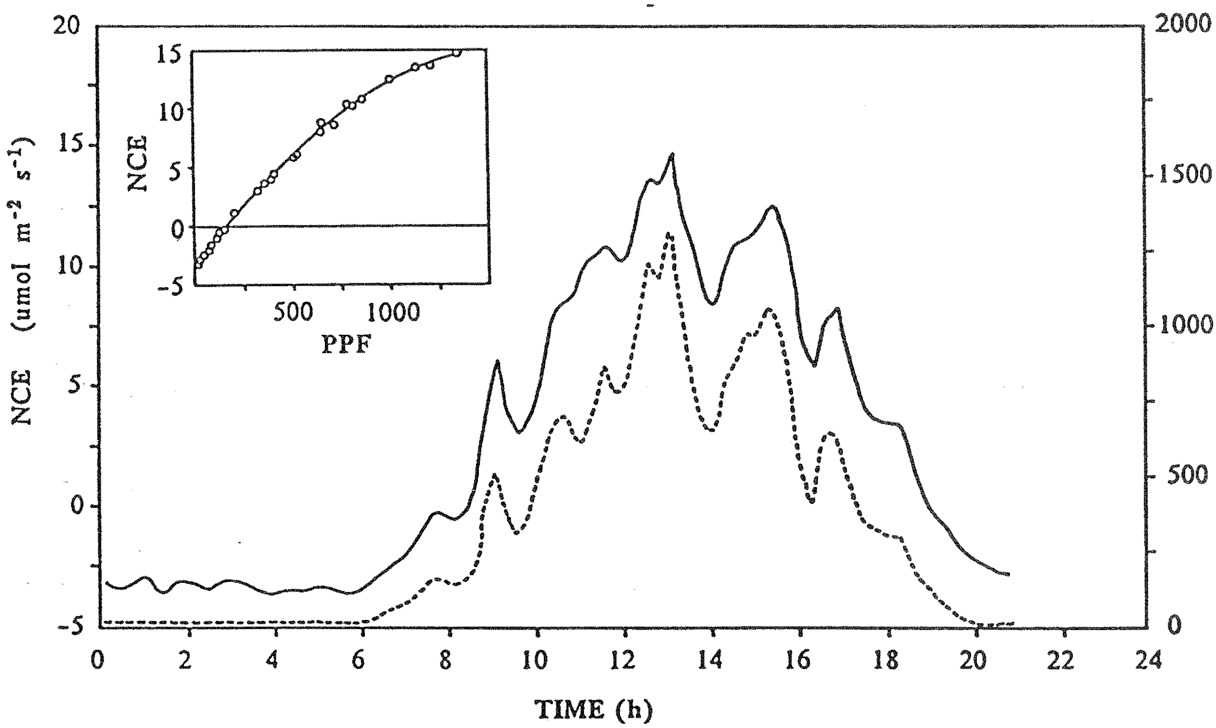

Figure 3.3. Diurnal trace of net ecosystem photosynthesis (NCE) and incident photosynthetic photon flux (PPF) in the monospecific stand of Scirpus olneyi, 29 May, 1987.

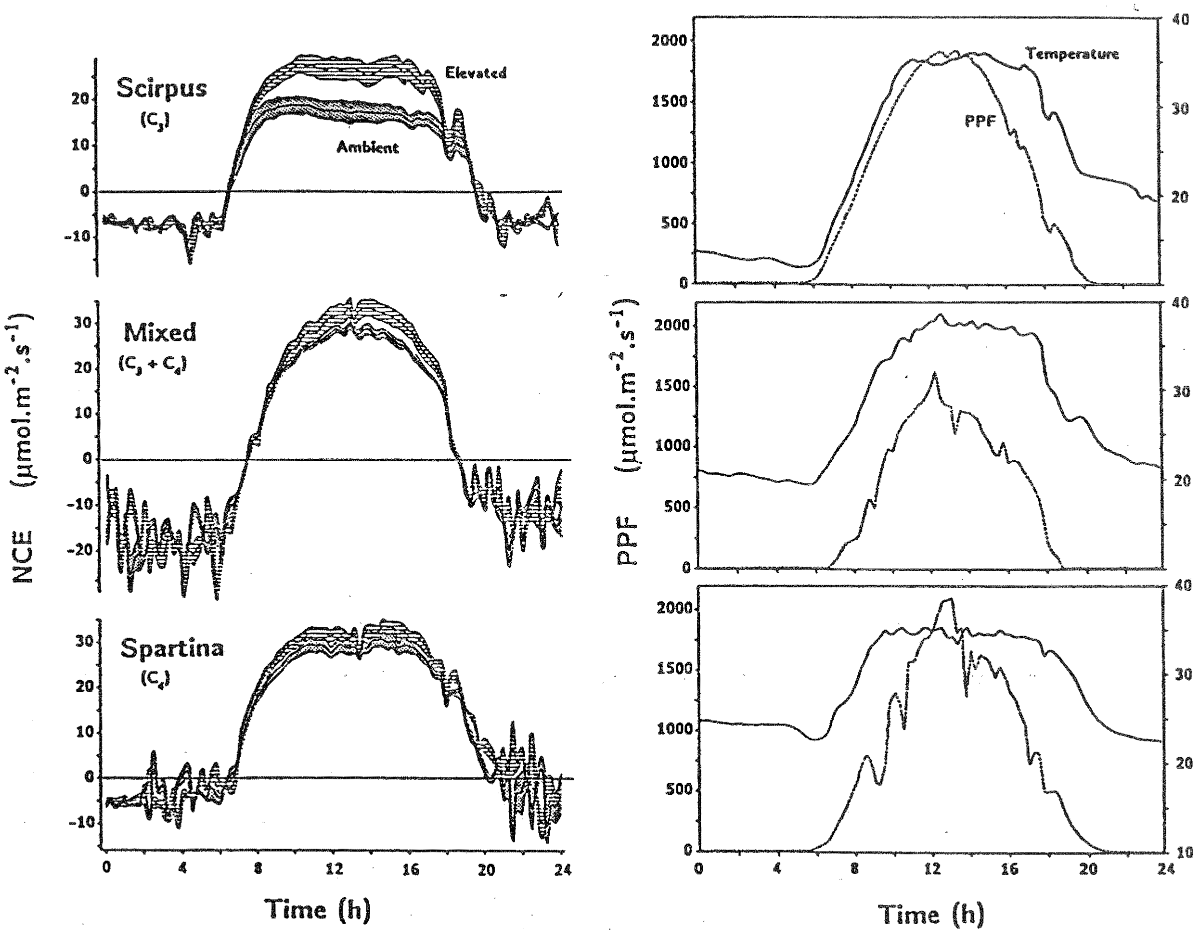

Figure 3.4. Net ecosystem photosynthesis, air temperature within one of the chambers, and incident PPF. Data for NCE are the means and 95% confidence intervals about the means for 5 chambers in elevated CO_2 and 5 chambers in normal ambient CO_2 in each community. Measurements for Scirpus made 29 June, for Mixed 11-12 July, and for Spartina 8 July.

the five chambers at elevated CO_2 were compared with the mean of the five values for the chambers at ambient CO_2 at each light level and ß value from these means was determined as follows:

$$\beta = (E - A) / A$$

where E is the mean value of NCE for all five chambers at a single value of PPF in elevated CO_2 and A is the mean value of NCE at that value of PPF in ambient CO_2. The ß values were then plotted against PPF for the three communities and the results of this shown in Fig 3.5A. This analysis shows that the response of NCE in the C_3 sedge to CO_2 increases from about 50% at low PPF (500 umol m^{-2} s^{-1}) to about 80 % at maximum PPF (2000 umol m^{-2} s^{-1}).

4. Interaction of temperature and CO_2 on NCE.

The effect of temperature on NCE in the <u>Scirpus</u> community was determined as follows. Measurements were made in two chambers during the course of the five day period, 17-21 July 1987. Only the data collected during the two hours on either side of solar noon (ca. 13:00 h) were used. These were separated into classes of time intervals of one hour and the ß values were computed as above for light where E is the value of NCE measured in the elevated CO_2 chamber, and A is the value of NCE measured in the ambient CO_2 chamber. Data were means of 15 minute intervals. The ß values are plotted in Figure 3.5B opposite temperature. The effect of temperature is evident above about 39 C and increases steeply. There is also an apparent effect of time: elevated CO_2 has about twice the effect in midafternoon that it has in the morning. This is because NCE at ambient CO_2 is decreasing with time but it is increasing or remains constant in elevated CO_2. What is varying with time is probably water potential: as the day progresses, leaf water potential declines.

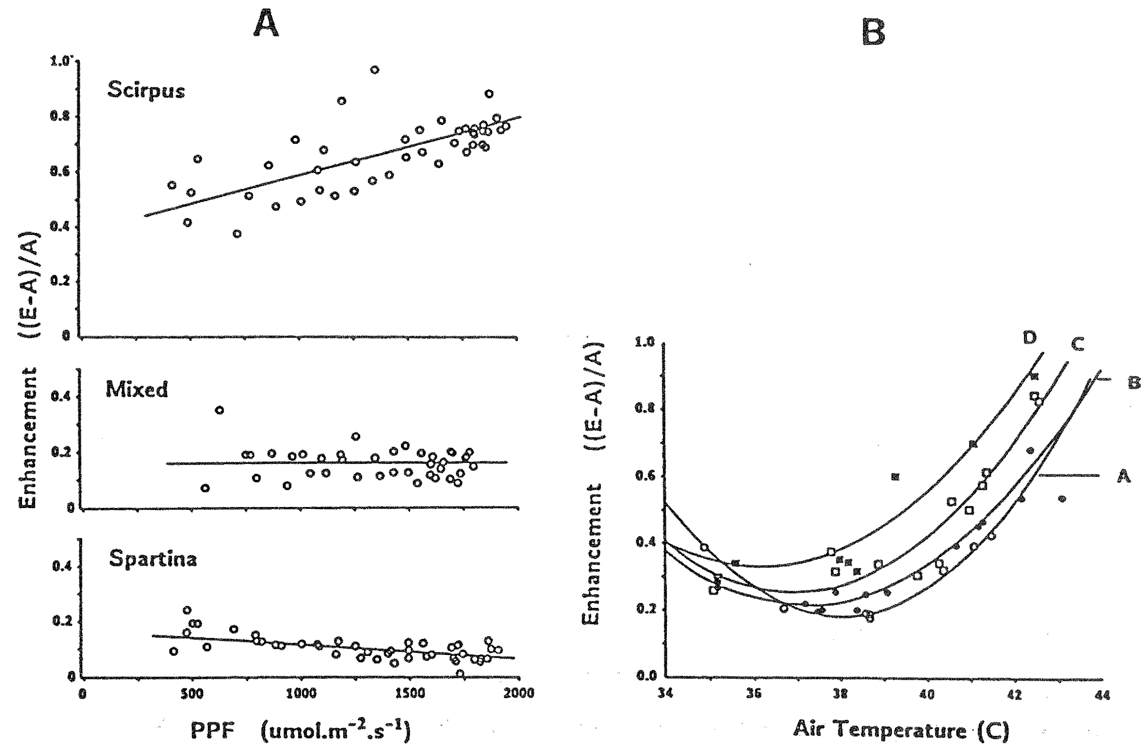

Figure 3.5 A) The effect of light on the stimulation of photosynthesis by elevated CO_2 in the three communities for the data shown in Figure 3.4. Each data point is a ß value computed with the mean NCE for elevated CO_2 chambers and the mean for ambient CO_2 chambers at each PPF value. A. _Scirpus olneyi_, B. Mixed, C. _Spartina patens_.

B) The effect of temperature on the stimulation of NCE by elevated CO_2 in the _Scirpus olneyi_ community. ß was calculated using data on NCE collected over a five day period, 17-21 July, 1987, in a chamber exposed to elevated CO_2 and one exposed to ambient CO_2. All values were obtained when PPF exceeded 1700 uMol/m2s. Data were further classified according to the hour between 11:00 and 15:00. Lines are quadratic equations fit to the data with R square values all greater than 0.91. Data for the effect of temperature on ß were grouped according to time, open circles (A) are data between 11-12:00 hrs; closed circles (B) between 12-13:00 hrs, open squares (C) between 13-14:00 hrs and closed squares (D) between 14-15:00 hrs.

5. Seasonal effects of elevated CO_2 on NCE.

The seasonal course of maximum net ecosystem CO_2 exchange is shown in Figure 3.6 in which the daily mean value of maximum NCE is plotted for the three communities from the end of May until the end of October. The highest values of NCE were recorded in elevated CO_2. They were highest in the *Scirpus* community where they sometimes exceeded 55 umol m^{-2} s^{-1} compared with about 40 umol m^{-2} s^{-1} in the mixed community and 35 umol m^{-2} s^{-1} in the *Spartina* community. The seasonal effect of elevated CO_2 was determined by plotting ß values computed for each day in each community in the right hand panels of Figure 3.6.

There was a clear seasonal response of photosynthesis of plant canopies. Maximum daily net CO_2 exchange (Pmax) is plotted in Figure 3.6. Throughout the growing season, the order of the enhancement effect of CO_2 on Pmax was *Scirpus*>Mixed>*Spartina* (Figure 2C). During spring and early summer, the enhancement of photosynthesis by elevated CO_2 was approximately 50% in the *Scirpus* community. There was also an enhancement effect of elevated CO_2 on the mixed and *Spartina* canopies but in the early part of the growing season up to about July, this response was less than 10%. After mid July, however, the relative enhancement of canopy photosynthesis by elevated CO_2 increased in all three communities and by September the relative improvement in carbon dioxide assimilation exceeded 100% in the *Scirpus* community.

The increase in the effect of CO_2 on NCE may be due to several interacting factors including temperature, delay of senescence, and relief of water stress all caused directly or indirectly by the CO_2 treatment. The data on single leaf photosynthesis discussed above were obtained during July and may not represent the physiological state of photosynthesis of the leaf tissue, especially in the C_4 grass, *Spartina patens* during

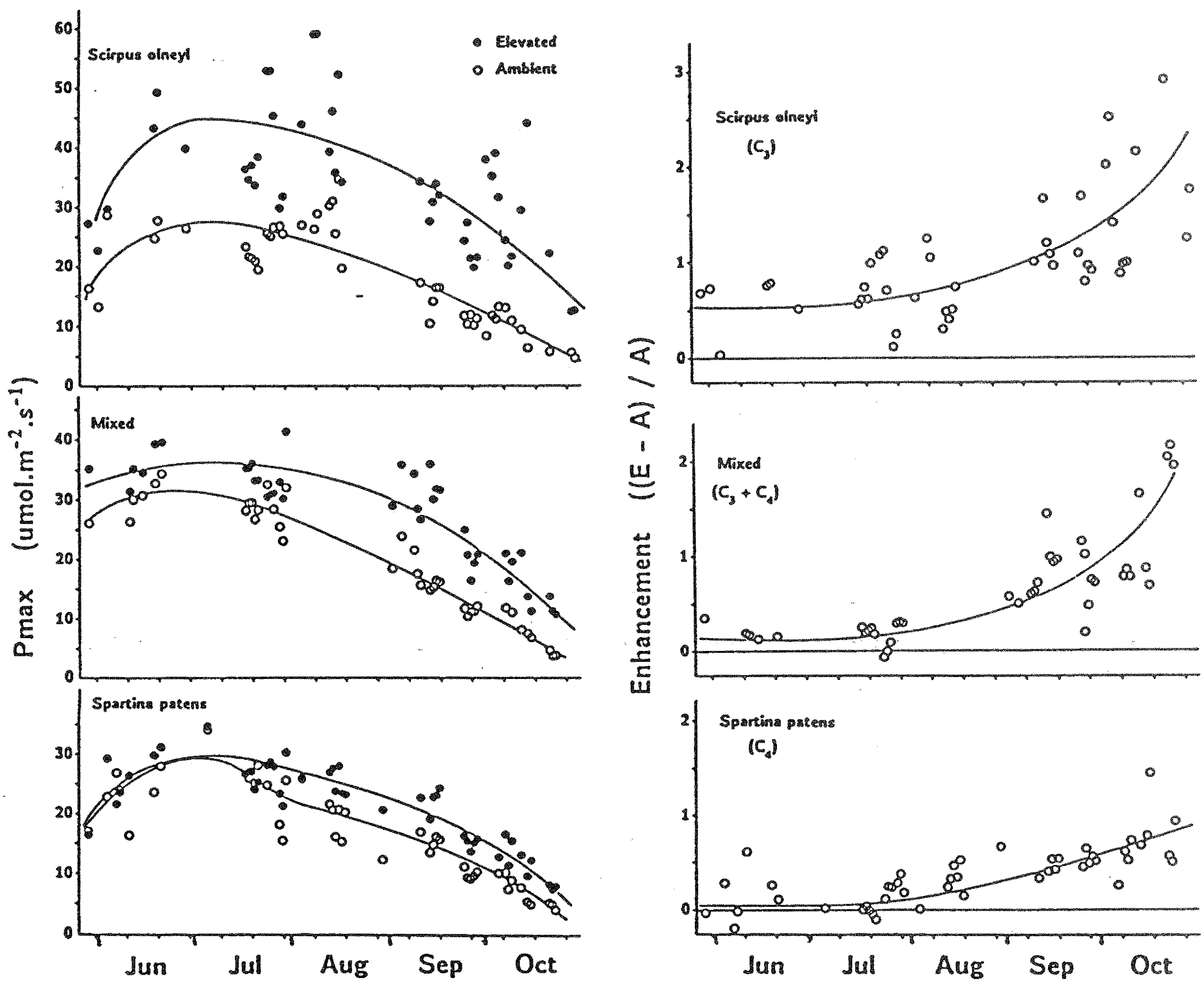

Figure 3.6. The seasonal effect of elevated CO_2 on the daily maximum NCE and on the ß (called enhancement here) computed for maximum NCE in each community.

late summer and autumn. There may also be different reasons for this effect in the different communities. The Scirpus community may be responding to a seasonal increase in salinity. Elevated CO_2 reduces the salt absorbed by the plant through the transpiration stream because less water is transpired. If salinity hastens senescence in Scirpus as it seems to do in other species (Walker, et al., 1983; Rush and Epstein, 1976) then growth in elevated CO_2 may delay the onset of senescence and this would explain the increase in the effect of elevated CO_2 on NCE as the season progresses into the warm, dryer, and more saline autumn. The difference between NCE in the elevated and ambient treatments may be due to combined effects of CO_2 on the physiological status of the plants as well as a difference in the total amount of green, healthy biomass present to assimilate CO_2.

Canopy architecture may play a role in the effects of CO_2 on the Spartina community. In the early part of the season, the Spartina community has a canopy architecture similar to the Scirpus community with leaves erect and stems vertical. After mid-July it changes to leaves horizontal and compressed which reduces photosynthesis about 50% (Turitzin and Drake, 1981). The increase in the enhancement of NCE by elevated CO_2 in the Spartina community coincides with this change in canopy leaf orientation and elevated CO_2 may simply overcome the additional resistance to diffusion of CO_2 imposed by compression of the canopy. Canopy compression would result in CO_2 depletion within the canopy which would be mitigated by doubling the CO_2 concentration above the canopy.

The effect of elevated CO_2 on integrated NCE was compared in the Spartina and Scirpus communities and the results are shown in Figure 3.7A and 3.7B. In Figure 3.7A, the total daily assimilation of CO_2 is used to compute a collective value for ß for each month. One ß value in this case is the mean value of NCE at elevated CO_2 for that day is used with the mean value for NCE

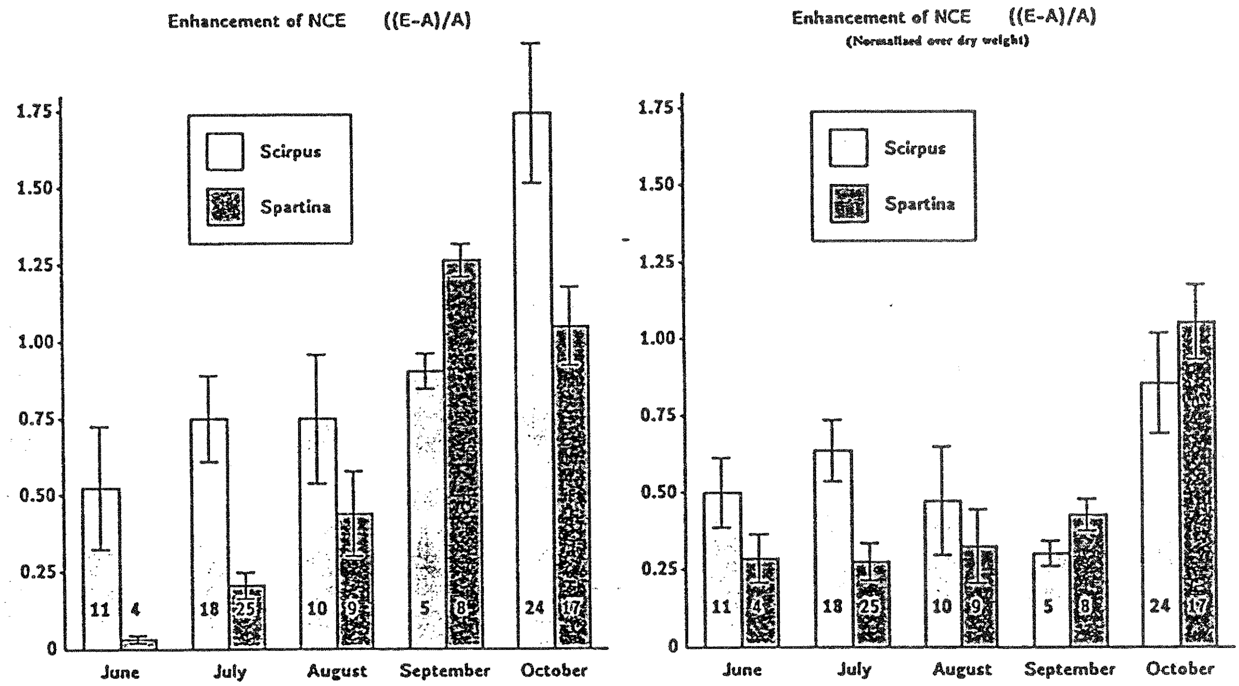

Figure 3.7. The effect of elevated CO_2 on daily integrated NCE for the mono-specific stands of <u>Scirpus olneyi</u> and <u>Spartina patens</u>. Each value of ß is computed on the mean daily value of NCE for each CO_2 treatment and the number of chambers used for any day varied from 2-5 per treatment. The number within the bar is the number of days for which a ß value was computed for that month and the bar length is the monthly mean values of ß. A. Integrated NCE per unit ground area; B. Integrated NCE per unit green biomass.

at ambient CO_2. There were different numbers of chambers used in the computation of the means and different numbers of ß values for each month (listed inside the bars in Figure 3.7A and B). In Figure 3.7B the NCE data were normalized on dry weight of green biomass present in the chamber.

The additional carbon assimilated during the last half of the season by the plants grown in the CO_2 treatment was probably stored belowground and may affect the growth of vegetation during the 1988 field season.

Data for integrated NCE along with the calculated dry weight inside the chamber, the total incident PPF for that day, and the integrated values of NCE normalized on dry weight and on PPF are given in Table 3.3 for each chamber and each day that data were recorded.

6. Integrated seasonal carbon balance from ecosystem gas exchange measurements.

A major objective of this study is to determine the total amount of carbon sequestered by the ecosystem. The dataset for 1987 was not sufficient to calculate a carbon budget for each chamber, but for a representative chamber pair in the Spartina community (Sp 13 & 14) and in the Scirpus community (Sc 1 & 2) the carbon sequestering was estimated. The amount of carbon sequestered was calculated as the total amount of carbon acquired by photosynthesis minus the amount lost by respiration during the season of 1987 (Table 3.2).
For each chamber days were selected on which a complete dataset for photosynthesis was available (Table 3.3). The integrated values for photosynthesis and PPF were calculated over the daytime period, and the factor E (ratio photosynthesis / PPF) was

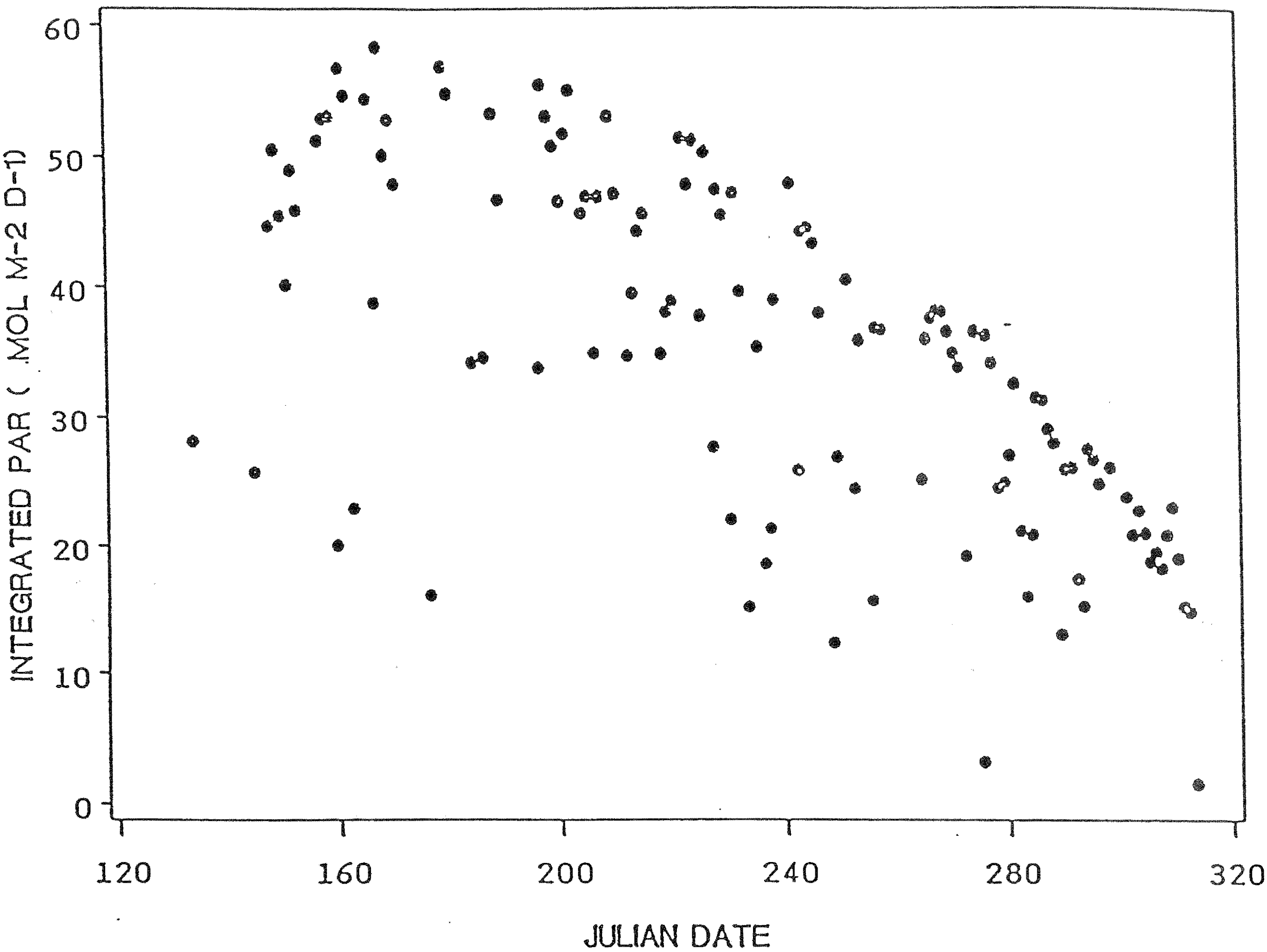

Figure 3.8. Integrated PPF for each day.

determined for each day. The relationship between E and julian date was estimated using a quadratic regression, and this regression was used to calculate a value of E for every day of the season. The integrated photosynthesis was calculated by multiplying E with the integrated PPF for each day (fig 3.8). These values were summed to give the total amount of CO_2 accumulated by photosynthesis during 1987.

For each chamber the mean respiration was calculated for every night on which good respiration data were available. The mean respiration for every night between April 1 and November 15 was estimated using a regression of mean respiration versus julian date. The mean respiration values were multiplied by the length of the dark period to obtain the total respiration for each night. These numbers were summed to give the total nighttime respiration for the 1987 season.

The enhancement of carbon sequestering due to elevated CO_2 is calculated as $(S_E - S_A) / S_A$ (S_E = C sequestered in elevated chamber, S_A = C sequestered in ambient chamber). This preliminary analysis shows an enhancement of 25% in Spartina and 106% in Scirpus.

Table 3.2. An estimate of the effect of elevated CO_2 on carbon sequestering in a Spartina and a Scirpus chamber pair. Peak biomass stands for the peak standing green biomass in August 1987. The units are g C m^{-2} $year^{-1}$.

Chamber	Peak Biomass	Photos.	Resp.	S (P − R)	Enhancement $(S_E-S_A)/S_A$
Spart Amb.	159.7	916.32	264.82	651.50	0.253
Spart El.	177.8	1129.91	313.51	816.40	
Scirp Amb.	464.6	1003.40	330.52	672.88	1.059
Scirp El.	527.6	1653.98	268.22	1385.76	

Table 3.3. Dry weight (g), PPF ($mmol.m^{-2}.day^{-1}$), integrated daily NCE ($mmol.m^{-2}.day^{-1}$), NCE per unit dry weight ($mmol.g^{-1}.m^{-2}.day^{-1}$), and NCE per unit dry weight and PPF ($umol.g^{-1}.mol^{-1}$) for the *Scirpus* and *Spartina* community.

JD	DW	PPF	NCE	NCE_{dw}	$NCE_{dw,ppf}$
Scirpus 1 Elevated					
179	760.1	.	1412.1	1.86	.
180	773.5	57065	1213.1	1.57	27.5
205	906.1	45832	1492.0	1.65	36.0
206	907.5	47081	1385.3	1.53	32.4
207	908.8	35121	1130.1	1.24	35.4
221	921.1	39027	1366.8	1.48	38.0
275	955.2	36720	1034.3	1.08	29.4
278	957.3	34309	855.5	0.89	26.1
279	958.1	24732	902.6	0.94	38.1
293	969.0	17601	593.9	0.61	34.8
294	969.8	15484	422.8	0.44	28.2
295	970.6	27643	481.4	0.50	18.0
Scirpus 2 Ambient					
179	740.4	.	947.1	1.28	.
180	750.0	57065	863.9	1.15	20.2
205	838.2	45832	937.0	1.12	24.4
206	838.4	47081	824.6	0.99	20.9
207	838.4	35121	740.4	0.88	25.1
221	830.8	39027	739.8	0.88	22.6
275	750.9	36720	300.1	0.40	10.9
278	745.3	34309	301.3	0.40	11.7
279	743.4	24732	322.6	0.43	17.3
293	715.5	17601	166.3	0.23	13.2
294	713.4	15484	127.2	0.18	11.6
297	707.1	25050	60.8	0.09	3.5
Scirpus 6 Elevated					
179	651.5	.	981.0	1.51	.
180	673.3	57065	696.5	1.04	18.1
210	916.7	53216	1033.0	1.13	21.2
211	917.3	47272	1389.9	1.52	32.1
225	913.8	51359	973.3	1.06	20.7
226	913.1	37932	1212.7	1.33	35.0
227	912.3	50483	1023.9	1.12	22.2
228	911.5	27885	874.6	0.96	34.5
275	853.5	36720	702.5	0.83	22.5
278	848.9	34309	615.1	0.72	21.1
279	847.4	24732	679.0	0.80	32.3
302	809.3	23998	215.9	0.26	11.0
303	807.6	21043	196.1	0.24	11.6
304	805.8	22970	260.3	0.32	14.1
Scirpus 4 Ambient					
179	687.8	.	1102.3	1.60	.
180	693.2	57065	930.1	1.34	23.5
210	723.7	53216	827.3	1.14	21.5
211	723.2	47272	1043.3	1.45	30.6
225	714.2	51359	922.9	1.29	25.2
226	713.5	37932	1102.3	1.54	40.7
227	712.7	50483	892.3	1.25	24.7
228	711.9	27885	696.0	0.98	35.0
278	663.6	34309	461.2	0.70	20.3
279	662.5	24732	490.8	0.74	30.1
302	633.9	23998	160.8	0.25	10.6
303	632.5	21043	152.7	0.24	11.4
304	631.2	22970	201.2	0.32	13.8

Table 3.3 (cont)

JD	DW	PPF	NCE	NCE_{dw}	$NCE_{dw,ppf}$
Scirpus 9 elevated					
151	98.5	40337	302.6	3.09	76.5
179	642.5	.	1209.0	1.88	.
180	660.6	57065	948.4	1.44	25.2
198	829.0	55684	882.3	1.06	19.1
199	832.0	53217	1072.0	1.29	24.2
200	834.7	50975	1034.8	1.24	24.4
201	836.9	46725	894.3	1.07	22.9
202	838.9	51868	1029.8	1.23	23.7
221	841.8	39027	1039.1	1.24	31.7
268	781.7	38256	637.3	0.82	21.4
269	780.1	38223	612.1	0.78	20.5
270	778.5	36700	599.4	0.77	21.0
271	776.9	35074	597.0	0.77	22.0
272	775.2	34021	645.9	0.84	24.5
282	758.3	32744	530.9	0.70	21.5
283	756.5	21378	570.7	0.75	35.3
284	754.8	16248	490.4	0.65	40.0
285	753.0	21098	498.2	0.66	31.3
286	751.2	31650	587.1	0.78	24.8
302	721.1	23998	235.5	0.32	13.5
303	719.2	21043	174.2	0.24	11.6
304	717.2	22970	264.9	0.37	16.2
Scirpus 8 Ambient					
151	136.3	40337	225.8	1.66	41.1
179	652.9	.	794.6	1.22	.
180	664.8	57065	566.8	0.85	14.9
198	748.9	55684	599.1	0.80	14.4
199	748.9	53217	739.3	0.99	18.6
200	748.6	50975	701.3	0.94	18.4
201	748.2	46725	542.3	0.73	15.5
202	747.4	51868	547.5	0.73	14.1
216	722.3	45738	590.1	0.82	17.9
268	539.8	38256	313.5	0.58	15.3
269	535.4	38223	290.3	0.54	14.2
270	531.0	36700	265.2	0.50	13.6
271	526.6	35074	279.5	0.53	15.1
272	522.2	34021	343.9	0.66	19.3
282	476.3	32744	262.8	0.55	16.9
283	471.6	21378	245.8	0.51	23.8
284	466.8	16248	209.5	0.45	27.7
285	462.0	21098	242.5	0.52	24.9
286	457.1	31650	259.0	0.57	17.9
302	375.7	23998	72.6	0.20	8.2
303	370.4	21043	54.0	0.14	6.8
304	365.0	22970	63.1	0.17	7.1
Scirpus 10 Elevated					
151	129.1	40337	729.0	6.20	153.7
179	661.4	.	1384.3	2.09	.
180	674.9	57065	1134.4	1.68	29.5
205	784.2	45832	1731.0	2.21	48.2
206	783.7	47081	1689.7	2.16	45.8
207	782.1	35121	1311.3	1.67	47.7
225	757.4	51359	1378.1	1.82	35.4
226	755.5	37932	1629.9	2.16	56.8
227	753.5	50483	1428.6	1.84	36.4
228	751.5	27885	1192.9	1.58	56.8
275	631.7	36720	850.4	1.34	36.6
278	622.6	34309	674.3	1.08	31.5
279	619.5	24732	711.3	1.15	46.4
302	542.9	23998	231.8	0.43	17.8
303	539.3	21043	202.6	0.38	17.8
304	535.8	22970	282.7	0.53	23.0
Scirpus 12 Ambient					
151	80.4	40337	193.9	2.41	59.8
179	543.3	.	677.4	1.25	.
180	559.1	57065	480.5	0.86	15.1
205	696.8	45832	718.7	1.03	22.5
206	696.0	47081	660.7	0.95	20.2
207	695.0	35121	511.1	0.74	20.9
225	655.5	51359	632.5	0.96	18.8
226	652.6	37932	755.9	1.16	30.5
227	649.6	50483	609.7	0.94	18.6
228	646.6	27885	487.6	0.75	27.0
275	465.4	36720	201.3	0.43	11.8
278	451.5	34309	198.8	0.44	12.8
279	446.8	24732	186.4	0.42	16.8
302	331.1	23998	140.2	0.42	17.6
303	325.7	21043	52.8	0.16	7.6
304	320.3	22970	62.7	0.19	8.4

Table 3.3 (cont)

JD	DW	PPF	NCE	NCE_{dw}	$NCE_{dw,ppf}$
<u>Scirpus 14 Elevated</u>					
151	124.1	40337	523.2	4.22	104.6
169	456.5	50236	1399.9	3.07	61.2
179	636.2	.	1166.5	1.83	.
180	649.0	57065	976.2	1.50	26.3
198	741.3	55684	1021.8	1.38	24.7
199	741.4	53217	1294.2	1.75	32.8
200	741.3	50975	1314.3	1.78	34.8
201	740.8	46725	1151.9	1.56	33.3
202	740.2	51868	1178.7	1.59	30.6
216	714.1	45738	1066.0	1.49	32.6
<u>Scirpus 15 Ambient</u>					
151	153.0	40337	172.8	1.13	28.1
169	453.9	50236	766.0	1.69	33.7
179	567.9	.	707.4	1.24	.
180	574.9	57065	513.3	0.89	15.6
198	619.1	55684	499.8	0.81	14.5
199	618.9	53217	623.2	1.01	19.0
200	618.5	50975	596.4	0.97	18.9
201	617.9	46725	488.6	0.79	17.0
202	617.3	51868	527.6	0.86	16.5
216	600.0	45738	621.3	1.03	22.6
275	464.2	36720	227.3	0.49	13.3
278	455.5	34309	201.3	0.44	12.8
279	452.5	24732	198.5	0.44	17.8
288	425.2	29227	120.8	0.28	9.7
289	422.1	28188	132.0	0.31	11.1
302	379.8	23998	42.5	0.11	4.7
303	376.4	21043	26.8	0.07	3.5
304	373.0	22970	48.2	0.13	5.5
<u>Spartina 1 Elevated</u>					
186	460.0	.	812.1	1.77	.
189	480.0	53477	1190.6	2.48	46.37
205	559.0	45832	808.6	1.45	31.57
206	562.0	47081	794.4	1.41	30.03
207	565.0	35121	637.1	1.13	32.12
225	602.0	51359	745.0	1.24	24.09
226	602.0	37932	784.7	1.30	34.38
227	602.0	50483	711.9	1.18	23.43
228	601.0	27885	485.9	0.81	28.99
268	403.0	38256	516.5	1.28	33.50
269	395.0	38223	451.9	1.14	29.92
270	385.0	36700	389.6	1.01	27.56
271	376.0	35074	407.4	1.08	30.91
272	368.0	34021	404.8	1.10	32.34
279	303.0	24732	310.0	1.02	41.36
<u>Spartina 2 Ambient</u>					
186	450.0	.	663.4	1.47	.
189	466.0	53477	1024.2	2.20	41.09
<u>Spartina 4 Elevated</u>					
158	286.0	53060	766.6	2.68	50.52
169	395.0	50236	909.7	2.30	45.86
186	498.0	.	854.1	1.72	.
189	510.0	53477	1292.0	2.53	47.38
198	528.0	55684	659.7	1.25	22.44
199	529.0	53217	839.9	1.59	29.84
200	530.0	50975	838.8	1.58	31.07
201	531.0	46725	655.7	1.23	26.41
202	531.0	51868	624.5	1.18	22.69
216	533.0	45738	595.4	1.12	24.40
241	527.0	.	392.5	0.74	.
245	511.0	44615	515.8	1.01	22.64
282	449.0	32744	270.6	0.60	18.42
283	445.0	21378	300.9	0.68	31.65
284	443.0	16248	271.4	0.61	37.68
285	441.0	21098	272.3	0.62	29.25
286	440.0	31650	338.5	0.77	24.30
158	320.0	53060	775.4	2.42	45.66

Table 3.3 (cont)

JD	DW	PPF	NCE	NCE_{dw}	$NCE_{dw,ppf}$
Spartina 5 Ambient					
169	430.0	50236	927.9	2.16	42.95
186	531.0	.	809.0	1.52	.
189	547.0	53477	1251.5	2.29	42.80
198	565.0	55684	672.8	1.19	21.37
199	567.0	53217	778.4	1.37	25.79
200	569.0	50975	790.0	1.39	27.25
201	570.0	46725	678.8	1.19	25.48
202	570.0	51868	776.6	1.36	26.26
216	575.0	45738	675.7	1.18	25.69
241	548.0	.	247.9	0.45	.
282	464.0	32744	193.0	0.42	12.69
283	461.0	21378	187.0	0.41	18.98
284	460.0	16248	150.7	0.33	20.18
285	458.0	21098	185.7	0.41	19.24
286	455.0	31650	229.5	0.50	15.91
Spartina 8 Elevated					
158	.	53060	.	3.69	69.47
186	.	.	.	1.92	.
189	.	53477	.	2.80	52.31
198	.	55684	.	1.64	29.43
199	.	53217	.	2.00	37.60
200	.	50975	.	2.06	40.40
201	.	46725	.	1.68	36.04
202	.	51868	.	1.74	33.59
216	.	45738	.	1.57	34.32
231	.	22293	.	0.41	18.20
241	.	.	.	0.38	.
242	.	48013	.	0.38	7.90
268	.	38256	.	0.86	22.57
269	.	38223	.	0.78	20.38
270	.	36700	.	0.75	20.38
271	.	35074	.	0.79	22.41
272	.	34021	.	0.85	24.91
293	.	17601	.	0.34	19.50
294	.	15484	.	0.38	24.86
295	.	27643	.	0.44	15.96
296	.	26887	.	0.34	12.74
297	.	25050	.	0.36	14.51
Spartina 9 Ambient					
158	.	53060	.	2.58	48.72
186	.	.	.	1.84	.
189	.	53477	.	2.43	46.28
198	.	55684	.	1.40	25.12
199	.	53217	.	1.64	30.78
200	.	50975	.	1.66	32.55
201	.	46725	.	1.45	31.04
202	.	51868	.	1.62	31.20
216	.	45738	.	1.21	26.36
231	.	22293	.	0.21	9.57
241	.	.	.	0.41	.
242	.	48013	.	0.45	9.31
268	.	38256	.	0.62	16.17
269	.	38223	.	0.56	14.56
270	.	36700	.	0.58	15.86
271	.	35074	.	0.55	15.55
272	.	34021	.	0.72	21.11
293	.	17601	.	0.13	7.38
294	.	15484	.	0.18	11.75
295	.	27643	.	0.21	7.70
296	.	26887	.	0.15	5.62
297	.	25050	.	0.14	5.20

Table 3.3 (cont)

JD	DW	PPF	NCE	NCE_{dw}	$NCE_{dw,ppf}$
Spartina 10 Elevated					
158	150.0	53060	573.7	3.83	73.49
186	230.0	.	764.8	3.33	.
189	242.0	53477	1130.5	4.67	87.36
210	363.0	53216	594.3	1.64	30.75
211	371.0	47272	859.0	2.32	48.96
282	299.0	32744	262.3	0.88	26.78
283	293.0	21378	273.5	0.93	43.66
284	285.0	16248	234.0	0.82	50.54
285	280.0	21098	228.5	0.82	38.66
286	272.0	31650	285.8	1.05	33.20
Spartina 11 Ambient					
158	210.0	53060	645.5	3.07	57.94
186	415.0	.	772.6	1.86	.
189	426.0	53477	1139.1	2.67	50.00
210	480.0	53216	484.4	1.01	18.97
211	481.0	47272	756.0	1.57	33.23
241	443.0	.	105.3	0.24	.
242	440.0	48013	119.9	0.27	5.68
282	293.0	32744	132.5	0.45	13.80
283	290.0	21378	122.8	0.42	19.78
284	286.0	16248	89.6	0.31	19.26
285	282.0	21098	114.5	0.41	19.26
286	278.0	31650	146.7	0.53	16.70
Spartina 14 Elevated					
186	397.0	.	693.2	1.75	.
189	402.0	53477	1103.5	2.75	51.34
205	412.0	45832	689.7	1.67	36.54
206	412.0	47081	698.9	1.70	36.05
207	411.0	35121	523.4	1.27	36.23
226	409.0	37932	625.8	1.53	40.32
227	408.0	50483	574.6	1.41	27.90
228	408.0	27885	383.7	0.94	33.75
268	368.0	38256	324.6	0.88	23.04
269	367.0	38223	302.2	0.82	21.55
270	364.0	36700	311.2	0.85	23.31
271	361.0	35074	324.9	0.90	25.65
288	328.0	29227	199.3	0.61	20.79
289	326.0	28188	208.3	0.64	22.68
Spartina 13 Ambient					
186	297.0	.	568.8	1.92	.
189	315.0	53477	919.3	2.92	54.58
205	377.0	45832	561.0	1.49	32.45
206	379.0	47081	487.5	1.29	27.31
207	380.0	35121	346.6	0.91	25.97
225	377.0	51359	445.2	1.18	22.99
226	374.0	37932	481.1	1.29	33.94
227	371.0	50483	366.9	0.99	19.58
228	369.0	27885	267.5	0.72	26.02
269	257.0	38223	148.0	0.58	15.07
270	253.0	36700	146.9	0.58	15.84
271	249.0	35074	147.0	0.59	16.85
272	248.0	34021	170.2	0.69	20.16
288	197.0	29227	107.8	0.55	18.72
289	192.0	28188	102.3	0.53	18.91

CHAPTER 4

PLANT NITROGEN AND CARBON DYNAMICS

Aboveground plant material harvested during serial censuses and belowground roots and rhizomes taken from regrowth cores were analysed for total nitrogen and carbon with a Carbon-Hydrogen-Nitrogen analyser (Control Equipment Corp.) at the University of Maryland, Horn Point Laboratory. Nitrogen and carbon content were calculated on a % by weight basis. Similar results were obtained when N was expressed on an area basis since there were no significant CO_2 effects on specific leaf weight (Chapter 2).

Canopy N was calculated as the product of aboveground biomass and %N of that tissue at a given census. Maximum aboveground N (M_N) and litter N (L_N) were calculated from the product of peak standing biomass and total litter biomass, respectively. The percentage of maximum aboveground N which was translocated out of senescing tissue was expressed as the recovery efficiency (R) (Melillo et al. 1984), where:

$$R = (M_N - L_N)/M_N \times 100$$

Results from the serial harvests were analysed for overall treatment effects using repeated measures analysis of variance. Single degree of freedom contrasts (Elevated vs Ambient, Ambient vs Control) within a harvest were made by univariate analysis of variance.

RESULTS

<u>Scirpus</u> shoots grown under elevated CO_2 had significantly less nitrogen than those exposed to normal ambient CO_2 concentrations in the pure and mixed communities (Table 4.1, 4.2, Fig 4.1A,B). The effect of CO_2 was not constant over the growing

season, with significant differences between Elevated and Ambient treatments first becoming apparent in June. CO_2 effects were again non-significant in November in the mixed community. There were no significant differences between Ambient and Control treatments at any time (Table 4.2). Percent carbon varied only slightly throughout the season and there were no significant effects on Scirpus in either community (Fig 4.1).

There were no significant CO_2 effects on leaf N in either C_4 species in the pure or mixed communities (Table 4.1, 4.2). The seasonal progression of leaf N in Spartina that is shown in Fig 4.1C is representative of both C_4 species from either community. Tissue N was high early in the season but fell sharply in late May to a fairly constant level of about 0.8%. In this instance, a small but significant difference in tissue N was observed in August. This was most likely due to unusually high N in the Ambient treatment rather than lower N under elevated CO_2 since Controls were also lower than Ambients at this harvest. No differences were seen in the other C_4 samples. Tissue C was similar to that in Scirpus and was unaffected by CO_2 (Fig 4.1C).

The decrease in tissue N in Scirpus under elevated CO_2 caused a significant increase in C/N ratios in both communities (Fig 4.2). Scirpus in pure stand showed a 20-30% increase in shoot C/N between August and November. In the mixed community the effect varied between a 20% and 40% increase in C/N. There was no significant effect of CO_2 on senescent tissue, however. Dead Scirpus shoots had higher C/N ratios than living shoots but there were no significant differences between Elevated and Ambient treatments (Fig 4.2).

Although tissue N was reduced in Scirpus from the pure community, increased growth under elevated CO_2 offset this reduction, resulting in no net effect on total canopy N (Fig 4.3A). Lower canopy N in mid-June was due to slightly lower

Table 4.1. Results of repeated measures analysis of variance testing for treatment effects on leaf nitrogen content in three salt marsh species. The relatively high F value in the *Spartina*-Pure community was due primarily to high tissue N content in Control sites at some harvests (see Table 4.2).

Species - Community	F	P <
Scirpus - Pure	4.82	.029
Scirpus - Mixed	19.53	.0004
Spartina - Pure	3.62	.076
Spartina - Mixed	0.62	.556
Distichlis - Mixed	1.07	.372

Table 4.2. Tissue nitrogen content (% by weight) in whole shoots and leaves of the three study species from Elevated, Ambient, and Control plots. Harvest dates correspond to those in Fig 1, Chapter X. Mean ± (s.e.), N = 5.

	Harvest Date				
	May	June	July	August	October
	% N : Shoot				
SCIRPUS					
Elevated	2.28 (.05)	1.82 (.08)	1.30 (.03)	0.95 (.02)	0.56 (.03)
Ambient	2.29 (.06)	1.88 (.03)	1.44 (.03)	1.12 (.02)	0.69 (.03)
Control	2.28 (.11)	1.90 (.08)	1.39 (.07)	1.09 (.04)	0.64 (.04)
SPARTINA					
Elevated	2.43 (.21)	1.24 (.09)	0.84 (.06)	0.67 (.02)	0.77 (.04)
Ambient	2.54 (.09)	1.20 (.07)	0.90 (.06)	0.79 (.03)	0.75 (.03)
Control	2.22 (.24)	1.25 (.08)	0.92 (.05)	0.68 (.03)	0.73 (.02)
MIXED-*Scirpus*					
Elevated		1.62 (.04)	1.23 (.08)	0.87 (.06)	0.88 (.06)
Ambient		1.88 (.07)	1.55 (.15)	1.23 (.08)	1.07 (.08)
Control		1.78 (.07)	1.70 (.07)	1.19 (.13)	1.29 (.17)
MIXED-*Spartina*					
Elevated	2.33 (.14)	0.97 (.08)	0.70 (.05)	0.71 (.03)	0.60 (.03)
Ambient	2.45 (.21)	1.09 (.05)	0.80 (.05)	0.66 (.04)	0.72 (.07)
Control	2.20 (.05)	0.98 (.04)	0.69 (.04)	0.72 (.03)	0.79 (.16)
MIXED-*Distichlis*					
Elevated	2.24 (.21)	1.08 (.05)	0.88 (.04)	0.83 (.05)	0.86 (.16)
Ambient	2.58 (.21)	1.23 (.11)	1.05 (.10)	0.83 (.03)	0.90 (.08)
Control	2.74 (.25)	1.19 (.17)	0.98 (.03)	0.98 (.06)	0.95 (.07)
	%N : Leaf				
SPARTINA					
Elevated		1.60 (.10)		0.85 (.04)	1.03 (.06)
Ambient		1.68 (.06)		1.00 (.03)	1.06 (.03)
Control		1.27 (.17)		0.83 (.06)	1.11 (.04)
MIXED-*Spartina*					
Elevated		1.17 (.08)		0.90 (.02)	0.93 (.02)
Ambient		1.45 (.08)		0.85 (.05)	0.99 (.08)
Control		1.29 (.06)		0.94 (.03)	1.10 (.13)
MIXED-*Distichlis*					
Elevated		1.82 (.09)		1.32 (.09)	1.54 (.09)
Ambient		1.87 (.14)		1.39 (.04)	1.57 (.10)
Control		1.92 (.15)		1.69 (.10)	1.55 (.13)

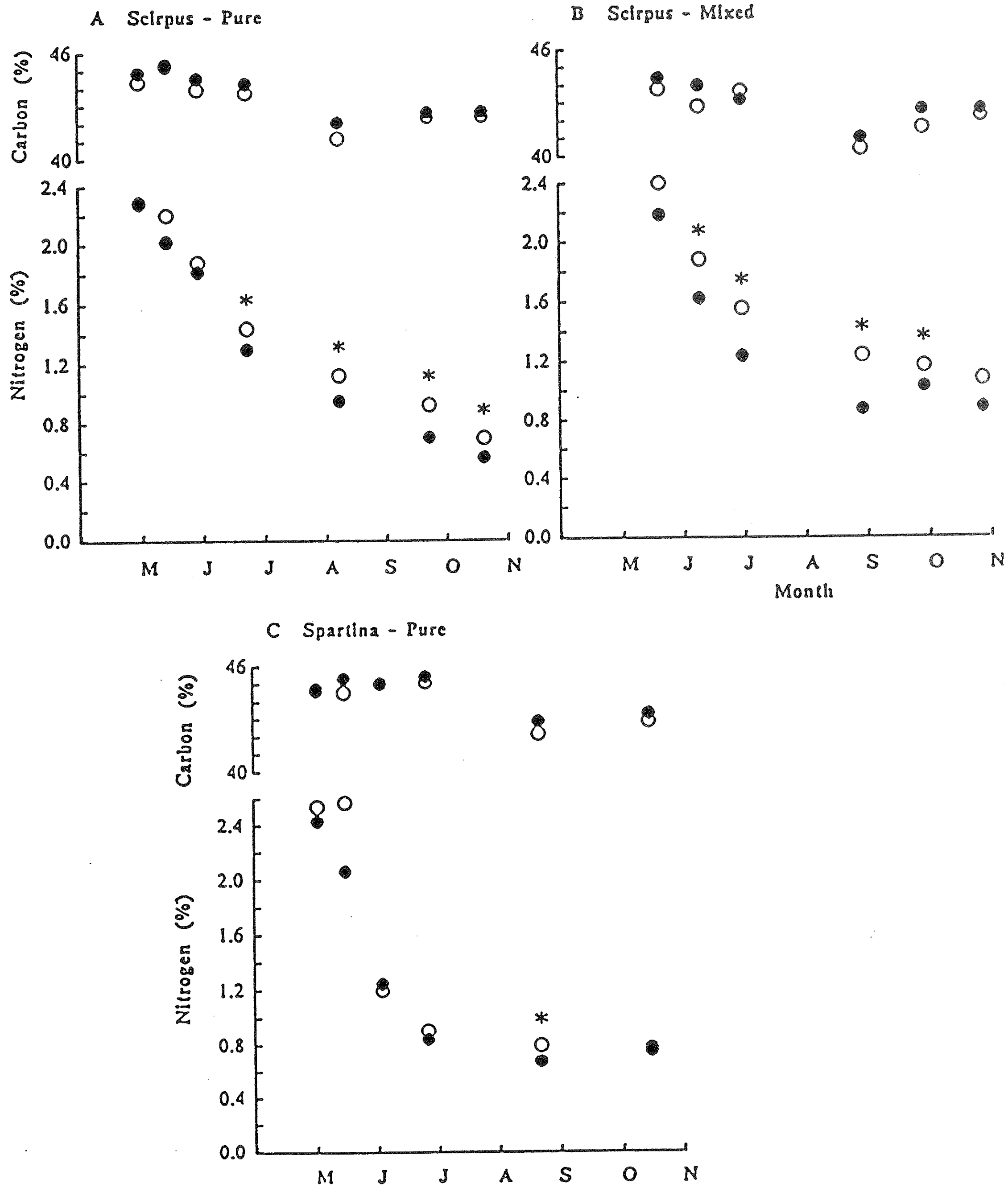

Figure 4.1. Percent carbon and nitrogen in aboveground tissue from Scirpus growing in pure stand (A), Scirpus growing in the mixed community (B), and Spartina growing in pure stand (C) under Elevated (●) and Ambient (○) CO_2 concentrations. Asterisk indicates significant difference ($P<0.05$) between treatments.

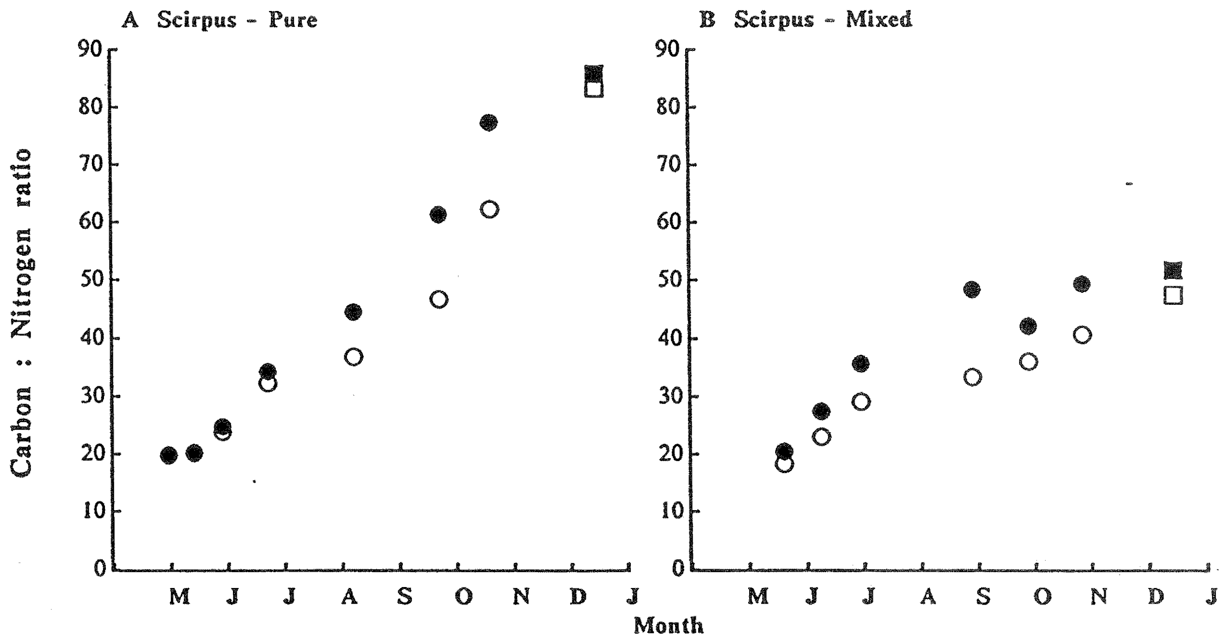

Figure 4.2. Carbon:Nitrogen ratio of green (●, ○) and senescent (■, □) tissue from <u>Scirpus</u> growing in pure stand (A), and in the mixed community (B). Plants were exposed to Elevated (shaded symbols) or Ambient (open symbols) CO_2 concentrations. Asterisk indicates significant difference ($P<0.05$) between treatments.

initial canopy biomass in Elevated sites. Total canopy N was not affected by elevated CO_2 in _Scirpus_ from the Mixed community (Fig 4.4A), in _Spartina_ (Fig 4.3B) and in the C_4 component of the Mixed community (Fig 4.4B). Total litter N, while unaffected by CO_2 in _Scirpus_ in pure stand, increased significantly ($P<0.05$) in _Scirpus_ from the mixed community. _Spartina_ had less than half the maximum aboveground N of _Scirpus_ in pure stand but left almost identical amounts of N in litter. This difference is reflected in the two fold difference in N recovery efficiency (Fig 4.5). Under ambient CO_2, _Scirpus_ in the mixed community had an N recovery efficiency intermediate between _Scirpus_ and _Spartina_ in pure stand. This was reduced under elevated CO_2, falling to below that found in _Spartina_.

Nitrogen and carbon content of belowground tissues exhibited much the same trends as the aboveground tissues. In _Scirpus_, roots and rhizomes had lower mean %N under elevated CO_2 (Table 4.3). There was no trend evident in %C or in either %N or %C in _Spartina_. Because of the small sample sizes these trends were not statistically significant. We have increased our sample size to correct this problem.

There was no difference in %C or %N of seeds from _Scirpus_ in pure stand between Elevated and Ambient treatments (Table 4.4). The enveloping bracts, however, behaved similarly to other shoot tissue, with significantly less N under elevated CO_2. There was a chamber effect in seed C and N, with Controls having higher %C and lower %N than Ambients.

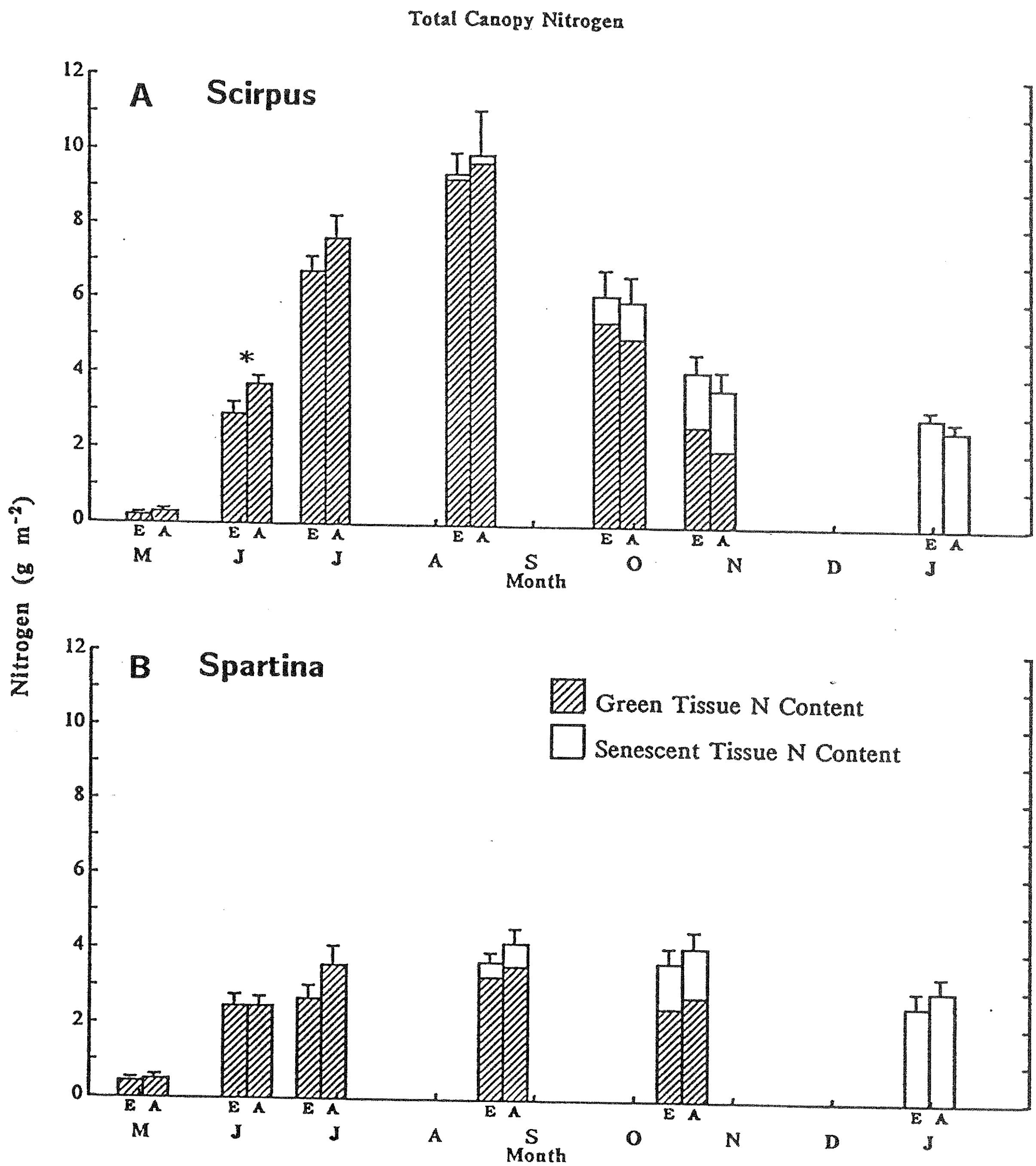

Figure 4.3. Total canopy N in pure stand Scirpus (A) and Spartina (B) under Elevated (E) and Ambient (A) CO_2 concentrations throughout the growing season. Total N is partitioned into that present in green tissue (shaded bars) or senescent tissue (open bars). Verical bars indicate one standard error.

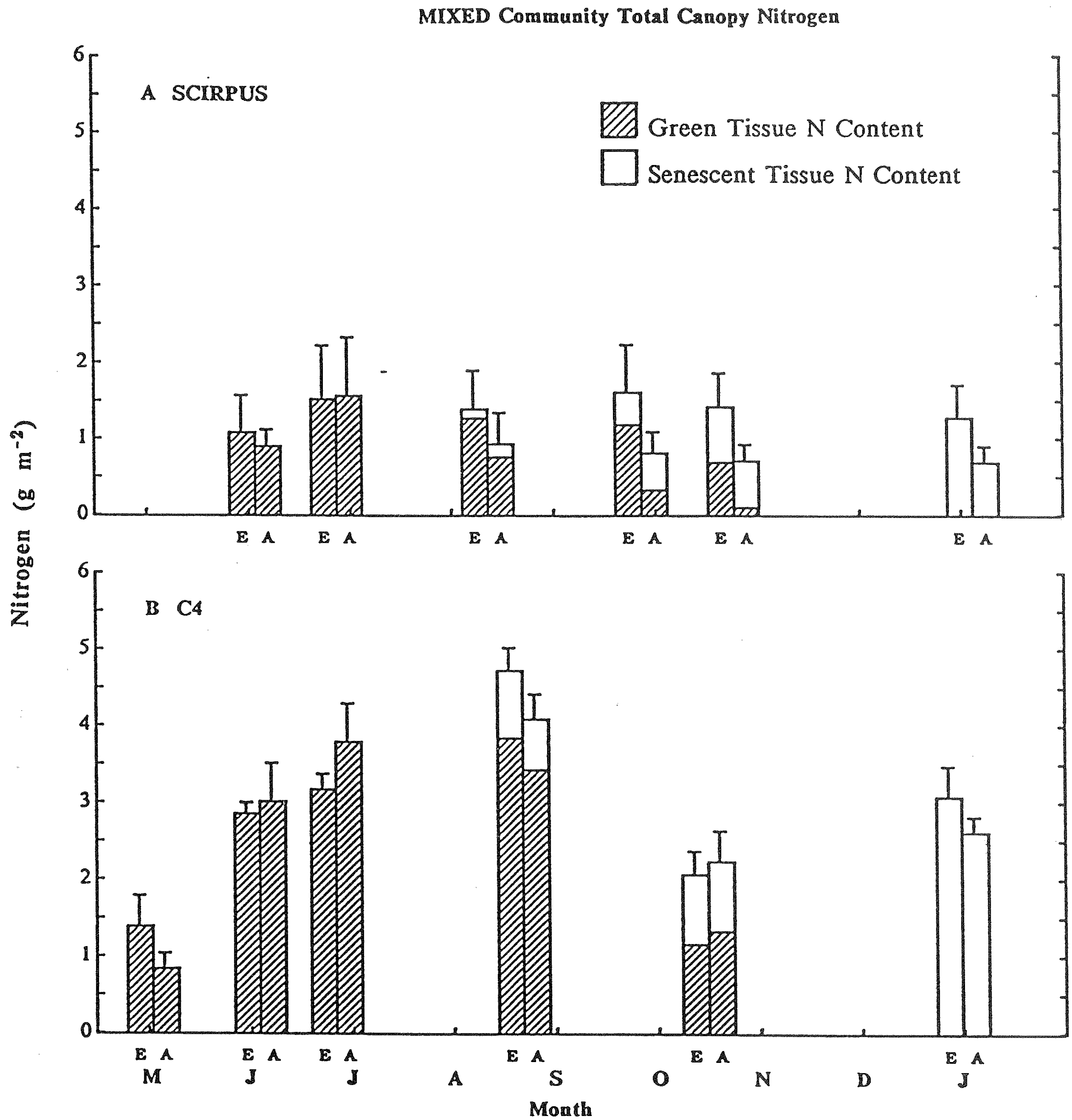

Figure 4.4. Total canopy N in the Mixed community Scirpus (A) or C_4 (Spartina + Distichlis) (B) under Elevated (E) and Ambient (A) CO_2 concentrations throughout the growing season. Total N is partitioned into that present in green tissue (shaded bars) or senescent tissue (open bars). Verical bars indicate one standard error.

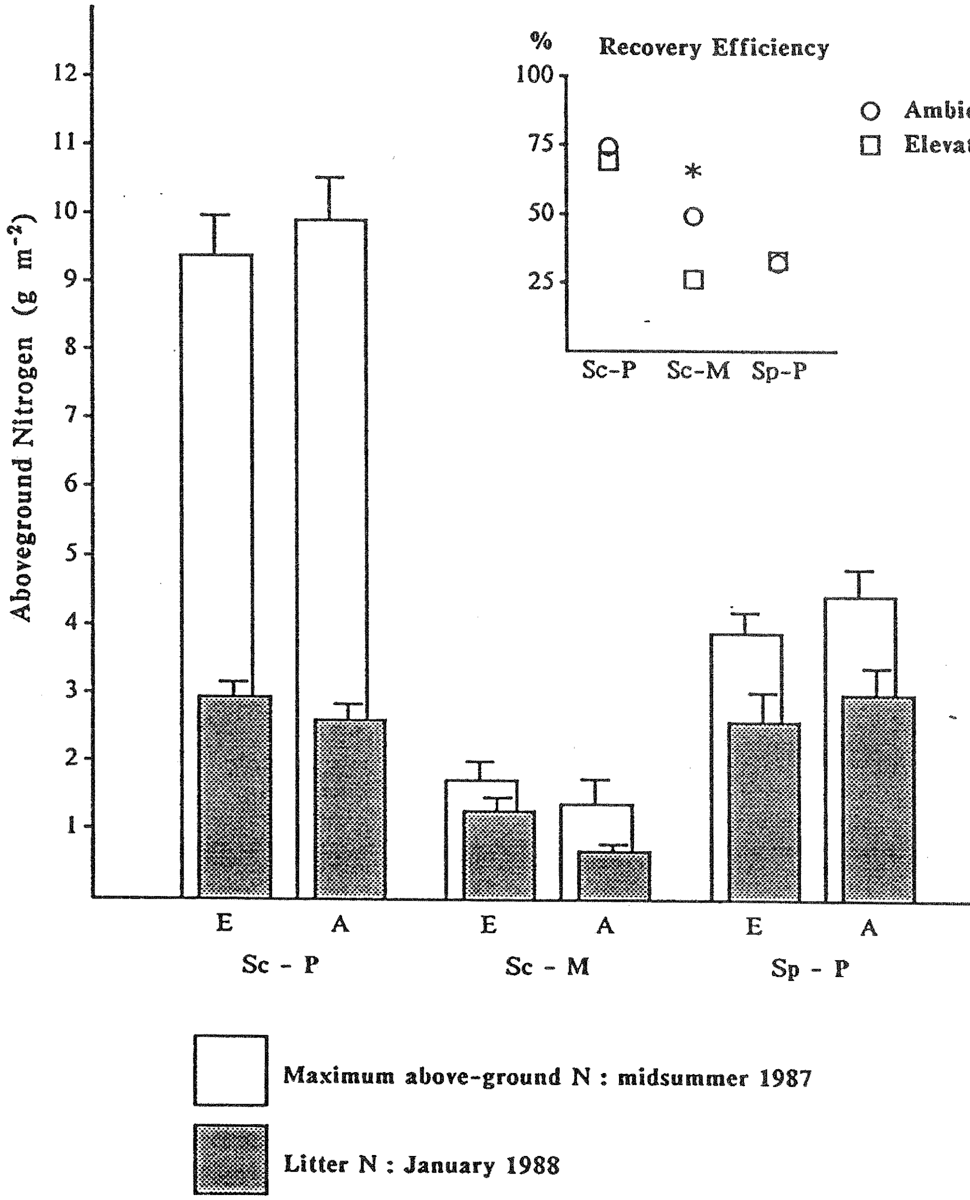

Figure 4.5. Maximum aboveground N in mature tissue (open bars) and in litter (shaded bars) from <u>Scirpus</u> (Sc) and <u>Spartina</u> (Sp) canopies in pure (P) and mixed (M) communities. Vertical bars indicate one standard error. Inset, recovery efficiency of N from mature tissue under Elevated (□) and Ambient (O) CO_2 concentrations. Asterisk indicates significant difference ($P<0.05$) between treatments.

Table 4.3. Carbon and nitrogen content of roots and rhizomes from regrowth cores of *Scirpus* and *Spartina* growing in pure stand. Mean ± (s.d.), n = 3.

		%C	%N
Scirpus			
Roots			
	Elevated	44.88 (.15)	.85 (.12)
	Ambient	44.39 (.27)	.93 (.15)
	Control	44.44 (.67)	.95 (.07)
Rhizomes			
	Elevated	44.44 (2.42)	.65 (.12)
	Ambient	43.71 (1.36)	.73 (.41)+
	Control	45.40 (--)	1.15 (--)*
Spartina			
Roots			
	Elevated	45.97 (.31)	.87 (.01)
	Ambient	46.04 (.38)	.95 (.08)
	Control	46.20 (.27)	.96 (.02)
Rhizomes			
	Elevated	46.02 (.25)	.78 (.08)
	Ambient	45.75 (.17)	1.17 (.32)
	Control	45.77 (.29)	.91 (.13)

+ n = 2, * n = 1.

Table 4.4. Carbon and nitrogen content of seeds and bracts from Scirpus growing in pure stand. Mean (± S.E.) n = 5.

		%C	%N
Seeds			
	Elevated	48.6 (0.3)[a+]	0.91 (0.11)[a]
	Ambient	48.9 (0.4)[a]	0.94 (0.11)[a]
	Control	49.6 (0.1)[b]	0.83 (0.04)[b]
Bracts			
	Elevated	45.1 (0.2)[a]	1.04 (0.04)[a]
	Ambient	45.2 (0.2)[a]	1.29 (0.04)[b]
	Control	45.8 (0.2)[a]	1.39 (0.04)[b]

[+] similar superscript denotes no significant difference, $P < .05$.

CHAPTER 5

PLANT WATER RELATIONS

Plant water relations were examined in field grown plants and in plants grown under controlled conditions at The Free University, Amsterdam. In the latter case, all plants were started from rhizomes collected from outside the study area in November, 1986. Water potential was measured with a pressure bomb.

Water use was measured in the lab by weighing all water inputs to the culture system and monitoring biomass accumulation. In the field, transpiration was measured with a water vapor analyser (BINOS) connected downstream of the CO_2 analyser. Sampling was fully automated and at the same frequency as for CO_2 analysis. In order for useful water vapor density data to be obtained, all components of the gas circuit had to be completely free of adsorbed water. This requirement limited the number of days that were sampled and the results should therefore be viewed as preliminary. Interstitial water salinity was measured with a refractometer. Water was pumped from 2 cm dia. PVC wells placed at various depths in 2 replicate plots from each treatment in each community.

Results

Elevated CO_2 resulted in significantly higher midday water potentials in all three study species (Fig 5.1, Table 5.1). Field and laboratory grown plants had very similar water potentials and experienced the same reduction of water stress midday under elevated CO_2. On average, shoot water potential increased about 0.5 MPa under elevated CO_2.

Plant water use decreased under elevated CO_2 in lab grown plants although this effect was not consistent across species (Fig 5.2). In the C_4 species, water use declined 15%-35% at low or high substrate salinity. In the C_3 species there was no reduction in water use at low salinity and a 15% reduction at high salinity. Transpiration was also reduced by elevated CO_2 in field grown plants. Figure 5.3 shows the water vapor density from elevated and ambient chambers in each community on a single day between 12:00 and 19:00 hrs. The effect of CO_2 was greatest from 12:00 to 16:00 hrs and was most pronounced in the C_4 species. When results from 5 days were averaged, however, this differential species response was no longer apparent (Fig 5.4). In both Scirpus and Spartina canopies there was a substantial increase in water use efficiency under elevated CO_2.

Interstitial salinity varied among communities and depths but showed no clear trend with respect to CO_2 treatment. In general, the Spartina community was the most saline, the Mixed community intermediate, and the Scirpus community the least saline (Table 5.2). The Scirpus community showed considerable heterogeneity, however, with plots on the north side of the boardwalk (Sc7,Sc8) being much more saline than plots on the south side (Sc1,Sc2,Sc3). Salinity was typically greatest at 30 cm, becoming almost fresh in some wells at 100 cm.

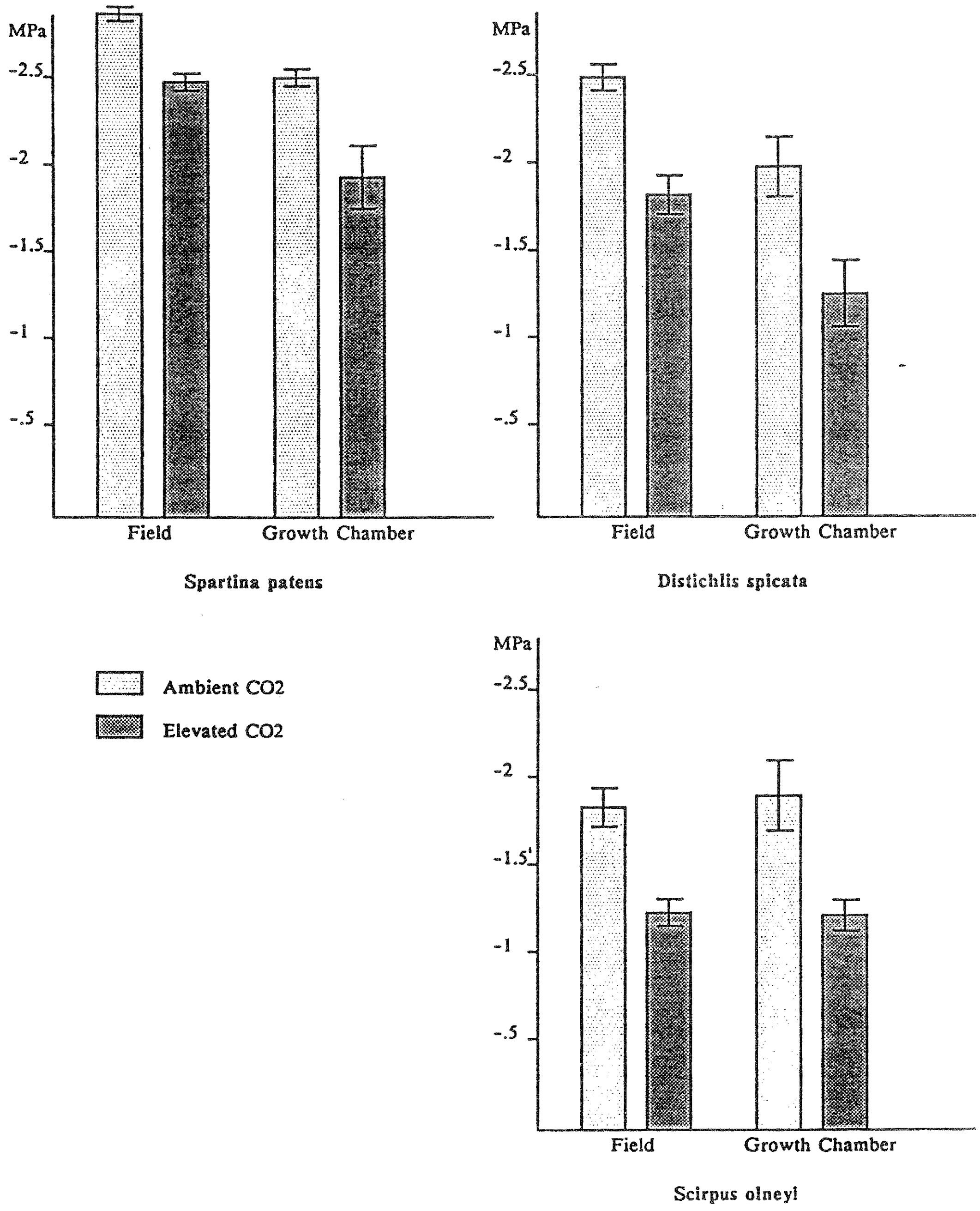

Figure 5.1. Shoot midday water potentials of field and growth chamber grown plants under elevated and ambient CO_2.

Table 5.1. Shoot midday water potentials of field grown plants. Treatments were Elevated CO_2 (E) and Ambient CO_2 (A).

			N	Mean	SD
29 May 1987					
	Distichlis	A	7	23.53	5.76
		E	6	19.6	5.02
	Spartina	A	8	20.81	2.55
		E	8	18.69	2.76
	Scirpus	A	4	12.13	4.84
		E	4	9.25	2.80
	Distichlis	A - E	6	5.03	1.10
	Spartina	A - E	8	2.12	1.76
	Scirpus	A - E	4	2.87	3.58
June 8 1987					
	Spartina	A	14	28.54	2.13
		E	14	24.71	1.45
	Spartina	A - E	14	3.82	2.84
29 June 1987					
	Distichlis	A	33	19.53	5.95
		E	32	13.05	4.38
	Distichlis	A - E	31	6.99	4.22
30 June 1987					
	Spartina	A	10	28.90	1.71
		E	10	24.98	1.95
		C	10	28.00	1.49
	Spartina	A - E	10	3.92	2.23
1 July 1987					
	Scirpus	A	10	18.48	3.49
		E	8	12.53	2.17
	Scirpus	A - E	8	5.68	3.44
4 August 1987					
	Spartina	A	3	39.00	2.24
		E	3	32.50	0.40
2 September 1987					
	Spartina	A	4	36.75	1.71
		E	4	31.96	2.96

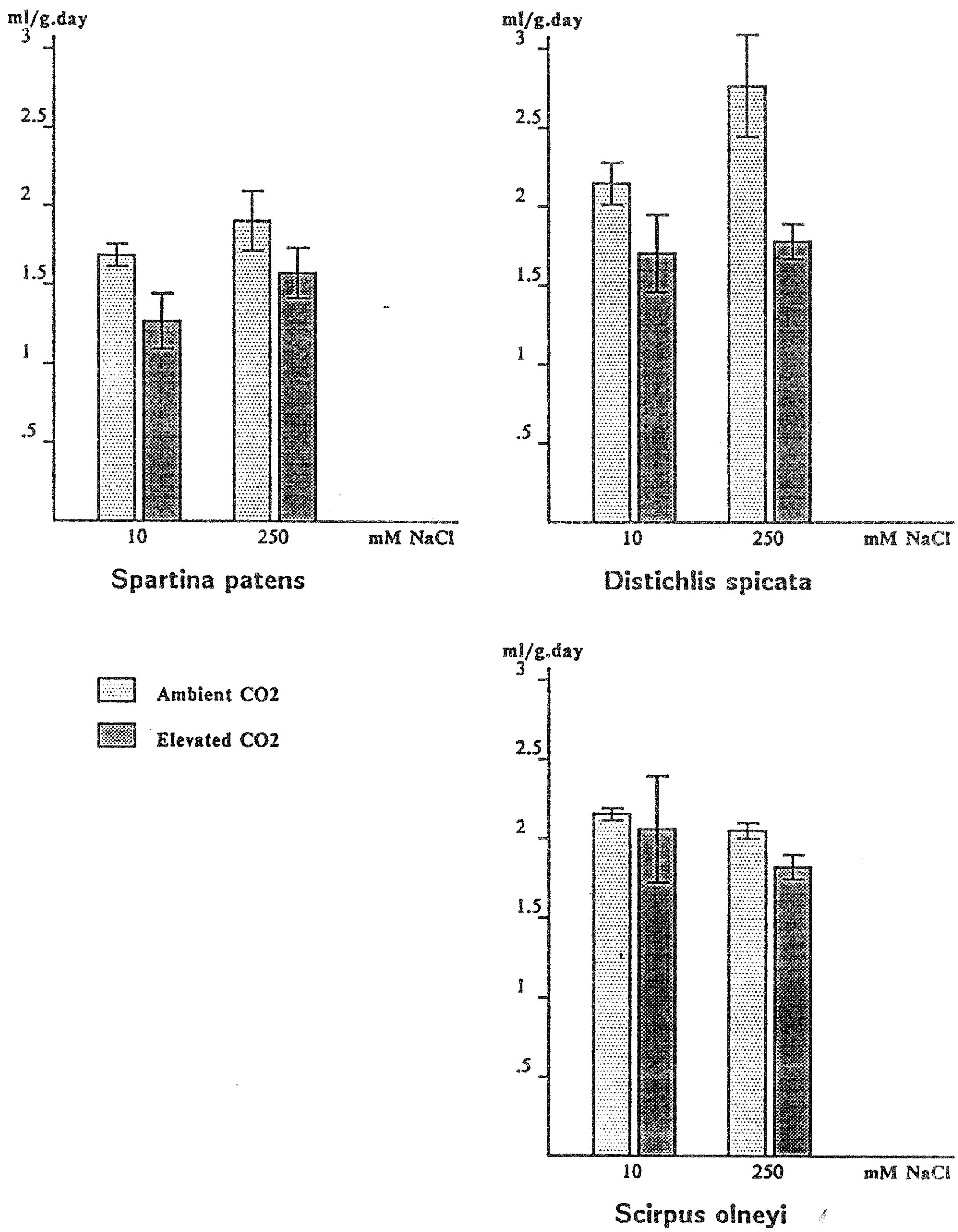

Figure 5.2. Water use per gram fresh weight of the three study species grown under controlled conditions at 10 or 250 mM NaCl and at ambient or elevated CO_2.

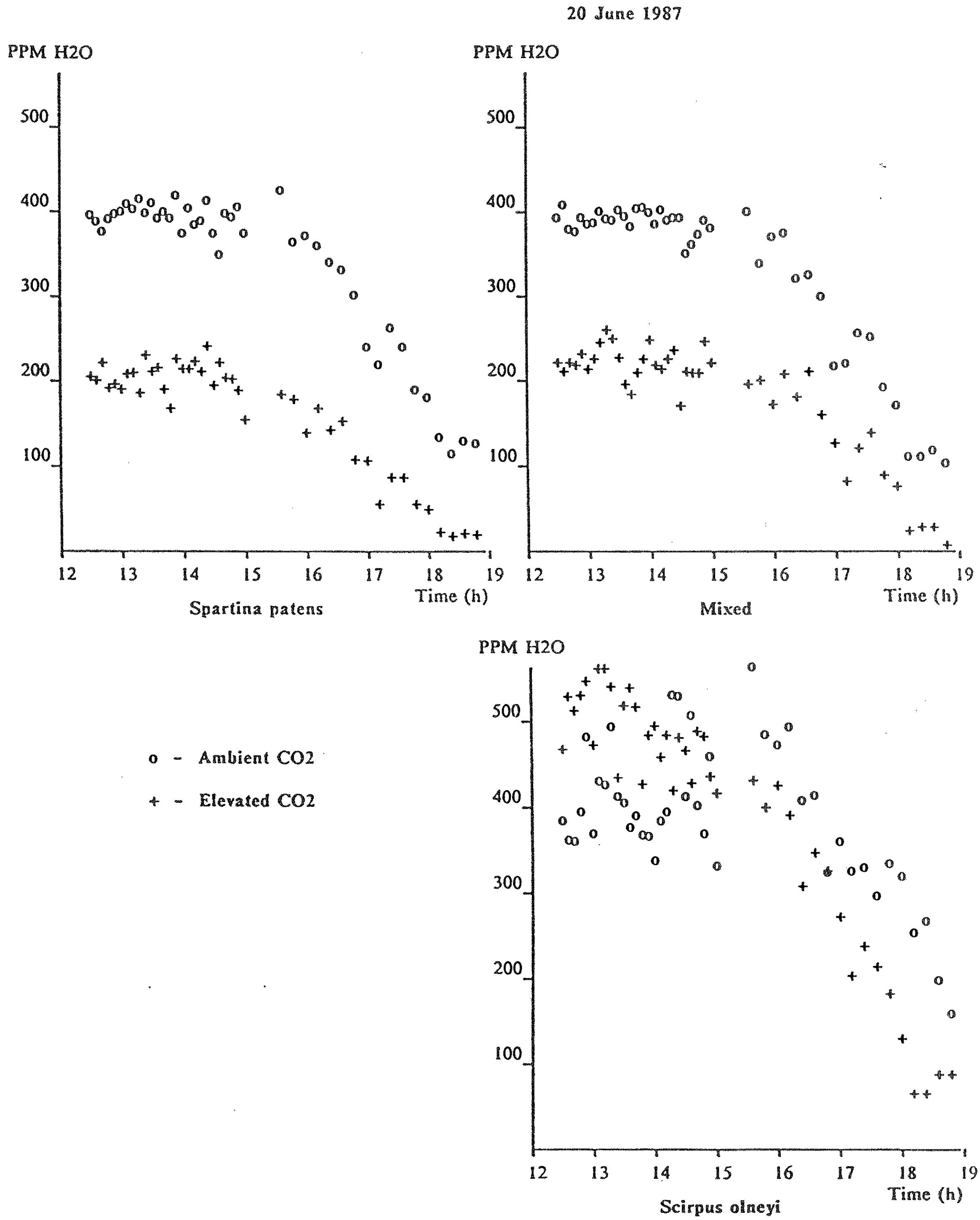

Figure 5.3. Water vapor density of sampled gas from elevated and ambient chambers in the three study communities.

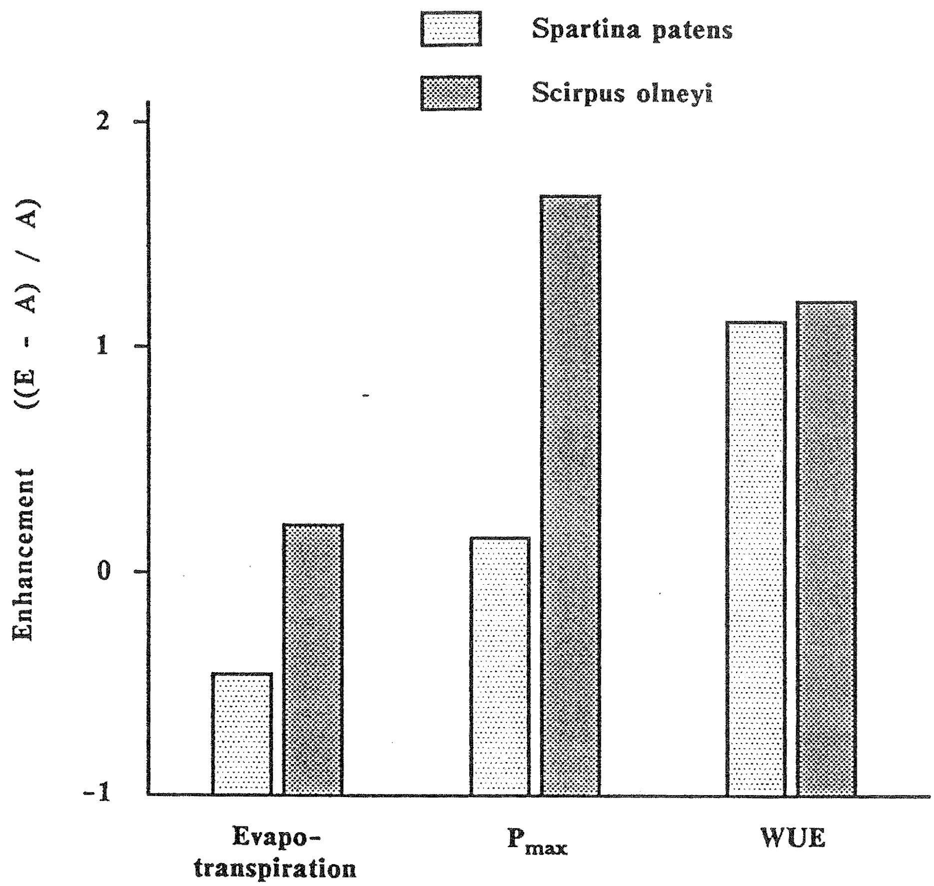

Figure 5.4. The enhancement effect of elevated CO_2 ((Elevated - Ambient) / Ambient) on evapotranspiration, photosynthesis and water use efficiency of Scirpus olneyii and Spartina patens.

Table 5.2. Interstitial salinity (ppt) from wells at four depths in <u>Spartina</u> (Sp), <u>Mixed</u> (Mi) and <u>Scirpus</u> (Sc) plots. Plot numbers and treatments (E = Elevated, A = Ambient, C = Control) are included.

	depth in cm.			
Site	15	30	50	100
6 May 1987				
Sp 04 E	7.8	10.5	8.0	4.5
Sp 05 A	11.8	12.2	11.2	4.8
Sp 06 C	10.0	11.2	9.8	3.8
Sp 10 E	8.8	10.8	9.8	5.8
Sp 11 A	7.5	9.8	8.8	6.8
Sp 12 C	7.8	10.2	9.5	5.2
Mi 01 E	8.8	10.0	5.8	2.0
Mi 02 A	9.8	8.0	4.2	1.5
Mi 03 C	10.8	7.0	5.8	2.0
Mi 10 C	4.0	6.0	2.5	1.2
Mi 12 A	10.5	4.5	4.0	1.0
Sc 01 E	6.2	6.5	3.8	1.0
Sc 02 A	4.5	4.8	2.8	0.8
Sc 03 C	5.0	4.0	2.0	1.2
Sc 07 C	5.2	10.0	8.8	6.2
Sc 08 A	9.0	12.2	12.5	7.8
15 May 1987				
Sp 04 E	7.8	10.0	7.2	3.5
Sp 05 A	11.5	13.2	11.8	4.2
Sp 06 C	8.8	11.2	8.5	3.0
Sp 10 E	9.2	10.8	9.8	5.2
Sp 11 A	8.8	10.0	9.0	5.2
Sp 12 C	8.0	10.0	9.0	5.0
Mi 01 E	8.8	9.8	5.2	1.0
Mi 02 A	8.8	5.5	4.2	1.0
Mi 03 C	9.8	7.2	5.8	1.5
Mi 10 C	3.8	5.8	2.0	1.0
Mi 12 A	9.8	7.2	4.0	0.8
Sc 01 E	6.2	6.8	2.8	0.8
Sc 02 A	5.2	4.2	2.5	1.2
Sc 03 C	4.8	3.8	2.2	1.0
Sc 07 C	5.2	9.5	10.0	6.8
Sc 08 A	8.2	12.2	12.2	8.0
6 June 1987				
Sp 06 C	6.0	10.0	9.0	3.0
Sp 10 E	10.0	10.0	10.0	6.0
Sp 11 A	10.0	10.5	10.0	6.0
Mi 01 E	7.0	7.0	4.5	1.0
Mi 02 A	6.0	7.5	4.0	2.0
Mi 03 C	9.0	7.0	4.5	2.0
Mi 10 C	1.0	2.5	5.0	0.5
Mi 12 A	8.0	6.5	---	1.0
Sc 01 E	7.0	6.0	4.0	1.0
Sc 02 A	5.5	5.0	2.0	1.0
Sc 03 C	6.0	3.0	2.0	1.0
Sc 07 C	8.5	10.0	10.5	7.0
Sc 08 A	9.0	11.5	12.0	7.5
29 July 1987				
Sp 04 E	10.5	9.8	6.0	3.2
Sp 05 A	12.2	12.0	11.0	4.5
Sp 06 C	12.0	7.0	8.2	3.2
Sc 01 E	8.5	5.2	3.5	2.2
Sc 02 A	10.0	5.0	2.2	1.2
Sc 03 C	8.8	5.0	2.5	1.2

GENERAL DISCUSSION

The most pronounced effect of the doubling in ambient CO_2 concentration on growth in these salt marsh communities was an increase in shoot numbers and decrease in the rate of senescence in the C_3 sedge, Scirpus olneyi. This resulted in a significant increase in live, aboveground biomass in the latter half of the season and greater net primary productivity in Scirpus from both the SCIRPUS and MIXED communities. These results support the prediction that plant growth in mature, unmanaged ecosystems containing C_3 species will increase in response to increasing atmospheric CO_2 concentrations (Bazzaz et al. 1985). We found no growth response in the SPARTINA community or the C_4 component of the MIXED community.

The increased shoot growth by Scirpus in the MIXED community did not have any detectible negative effect on Spartina and Distichlis but the long term consequences of a sustained growth response by Scirpus in this community are difficult to predict. Regions of the marsh with vigorous Scirpus populations have very little Spartina or Distichlis present. Competition as well as edaphic conditions are probably important in determining local species abundances on salt marshes (Snow and Vince 1984).

The slower rate of senescence and continued production of new shoots in Scirpus under elevated CO_2 resulted in a greater number of green shoots present in September and October, a slower relative rate of decline in aboveground biomass, and a lower percentage senescent tissue present in November.

The chambers had a significant effect on growth in the SCIRPUS community although there was no effect on Scirpus from the MIXED community or on the C_4 species. The 2° C temperature increase, protection of shoots from mechanical damage, and possibly higher humidity inside chambers could have contributed to the observed effects on growth.

We found a clear dichotomy in the effects of elevated CO_2 on shoot N in the C_3 and C_4 species. Increasing CO_2 reduced green tissue N in Scirpus but had no effect on Spartina or Distichlis. We found no evidence for increased carbon in Scirpus shoots although there were increases in both canopy and single leaf photosynthesis under elevated CO_2. This suggests that belowground rhizomes provided adequate sinks for the increased assimilation. Scirpus also showed no signs of photosynthetic acclimation or inhibition to elevated CO_2. The reduction in %N of Scirpus shoots resulted in an increase in green tissue C/N ratios of between 20 and 40%. Scirpus appears to preferentially allocate N into seeds since both the green shoots supporting the inflorescences and the bracts enveloping the seeds had lower N under elevated CO_2 but there was no reduction in seed N.

We found no evidence that exposure to elevated CO_2 led to an increase in total aboveground N. Rather, it appears that increased productivity in Scirpus under elevated CO_2 came at the expense of lower shoot N. While results from the first year of a long term study such as this can only indicate trends in ecosystem level processes, our data suggest that total N available for aboveground growth, and hence tissue N, may limit the potential for increases in productivity due to CO_2. We cannot at present say, however, to what extent N may be limiting current productivity.

Scirpus did not respond to the reduction in leaf N by increasing N recovery efficiency. In pure stand, Scirpus had a recovery efficiency of approximately 70%, similar to the maximum of 66% reported by Shaver and Mellilo (1984) for three marsh species grown at limiting available N, but there was no effect of CO_2. Recovery efficiency was lower in the mixed community where Scirpus was heavily shaded by Spartina and Distichlis and light may have been more important in limiting growth than N availability. Elevated CO_2 further reduced recovery efficiency in the mixed community resulting in more N lost in litter.

Midday shoot water potential was significantly higher in all 3 species under elevated CO_2, whether grown in the field or in the laboratory. Laboratory grown plants showed a decrease in water use per shoot while field grown plants had reduced transpiration and increased water use efficiency under elevated CO_2. An increase in water use efficiency through a combination of reduced transpiration and increased photosynthesis is perhaps the most general response of plants to elevated CO_2. Our data suggest that the stomatal response to high CO_2 might be even greater in the C_4 species than in the C_3. This improvement in water relations in the two C_4 species did not translate into improved growth during this first season.

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