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Progress Report of Research:

EFFECTS OF ELEVATED CO_2 ON CHESAPEAKE BAY WETLANDS.
IV. Ecosystem and Whole Plant Responses. April - November 1988.

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Chapter 1. Summary.

1988 was the second full year of treatment with elevated CO_2. The results obtained are interesting because 1988 was a very hot, dry year, one in which the effects of the drought should have played an important part in the response of plants to elevated CO_2. The main results obtained during the 1988 season are described below.

A. Growth and biomass production

1] Elevated CO_2 significantly increased the shoot density in the *Scirpus olneyi* (C_3) community. (fig 2.2, p 7); The increase in biomass in the elevated chambers was not statistically significant. A highly significant block effect was found in the *Scirpus* community, showing that environmental conditions are not homogeneous within the *Scirpus* community (fig 2.4, p 9).

2] No effect of elevated CO_2 was found on growth of *Spartina patens* (C_4) (fig 2.5, p 11).

3] In the mixed community growth of *Scirpus* was strongly enhanced by elevated CO_2, increasing the shoot density and biomass by 200 to 300 % (fig 2.7 p 15). Although *Spartina patens* and *Distichlis spicata* (C_4) showed no significant change at elevated CO_2 (fig 2.8, p 17; fig 2.9, p 19), there is evidence that the increase in *Scirpus* was at the expense of *Spartina* (fig 2.11, p21).

4] A large increase in *Scirpus* root biomass was found in the pure and mixed community (fig 2.12, p 23), but elevated CO_2 had no effect on the belowground biomass of the C_4 species (fig 2.13, p 24).

B. Nitrogen

Elevated CO_2 reduced the nitrogen content of aboveground tissue of *Scirpus* in both pure and mixed community, but not in aboveground tissue of *Spartina* (fig 3.1, p 39; tab 3.1, p 44). The nitrogen content of belowground tisues was reduced in all three communities (fig 3.3, p 43).

C. Photosynthesis

1] Elevated CO_2 increased single leaf photosynthesis of *Scirpus* (fig 4.1, p 52), but the effect on *Spartina* was smaller (fig 4.2, p 53) and occured only in the spring (fig 4.3, p 55).

2] There was no apparent acclimation of photosynthesis to elevated CO_2 for 1987 and 1988 (fig 4.1, p 52).

3] Elevated CO_2 increased canopy photosynthesis by 80% in *Scirpus*, 30% in *Spartina* and 13% in the mixed community (fig 5.4, p 64) when compared on the basis of ground area. On the basis of dry weight of green tissues, the response of the Scirpus community to CO_2 was almost constant at a 55% increase throughout the season (fig 5.5, p 66).

D. Respiration

Elevated CO_2 reduced canopy dark respiration of all three communities (fig 5.7, p 69) and respiration of single leaves in *Scirpus* (fig 5.8, p 70). Comparable results were obtained from a variety of other species (fig 5.9, p 72).

E. Carbon budget

Elevated CO_2 increased net seasonal carbon gain by 114% in *Scirpus*, 71% in *Spartina* and 22% in the mixed community (fig 5.11, p 79).

F. Evapo-transpiration

Evapo-transpiration was reduced in all three communities (fig 6.2, p 97), leading to an increase in the water use efficiency (fig 6.3, p 98) and an improvement of the water status in the plants (fig 6.6, p 102).

G. Competition

Elevated CO_2 increased the number of shoots and the aboveground biomass of the C_3 component (Scirpus olneyi) of the mixed community (fig 2.7, p 15; fig 2.6, p 13).

Chapter 2. Plant growth, reproduction and senescence.

To determine the effect of elevated CO_2 on growth processes during the second year of exposure, the vegetation was sampled four times in the *Scirpus* and *Spartina* community and three times in the mixed community. The methods used were largely the same as those used in 1987 and described in greenbook #044. A summary of the methods is given below as well as any new methods used in 1988.

Aboveground biomass.

Methods.

The *Scirpus* community was sampled four times during the 1988 growing season at which time the green and total length of each stem was measured and the reproductive status was recorded. During each census, five stems were harvested from each chamber and their widths, total lengths, green lengths, total dry weights and green dry weights measured. The specific leaf weight in *Scirpus* is calculated as the dry weight per area of one side of the triangular stem.

The relationships between total stem length and stem dry weight and between senescent stem length and weight were established using a quadratic regression forced through the origin (figure 2.1). The total and senescent dry weight of each stem in all of the chambers was then estimated using the length measurements and the regressions. The total biomass in each chamber was calculated by summing the estimated weights for all stems. Total green biomass was calculated by subtracting the estimated weight of the senescent biomass from the total biomass.

The *Spartina* community was also censused four times during 1988 by counting all living shoots in five permanent quadrates of 10x10 cm, and by harvesting all living shoots from five 5x5 cm quadrates. The harvested shoots were counted and separated into leaves, stems and senescent tissue prior to the determination of leaf area and dry weight. Shoot density per meter square was determined for each

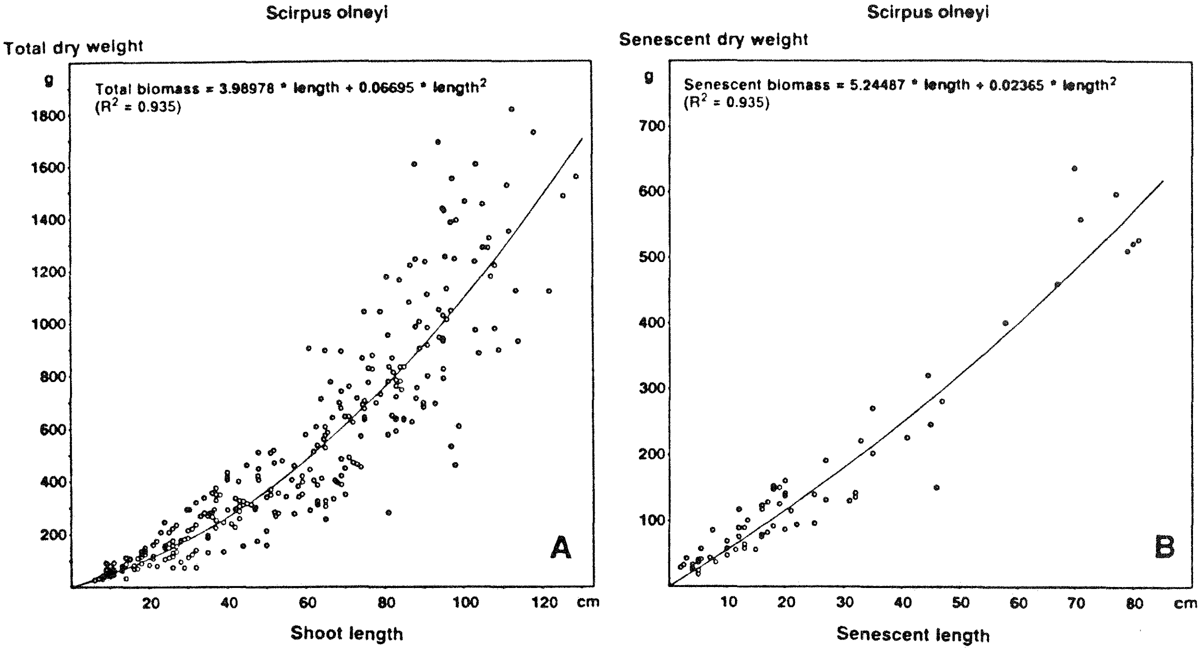


Figure 2.1. Length and weight of harvested *Scirpus olneyi* stems in 1988. The datapoints and the regression used for estimating total shoot weight are shown in A, the regression for senescent shoot length and weight is shown in B.

chamber by multiplying the number of shoots in the five 100 cm^2 quadrates by 20. The mean shoot dry weight per chamber was calculated as the sum of the dry weight of the leaves stems and senescent tissue divided by the number of shoots Total dry weight per meter square was calculated found by multiplying the mean shoot dry weight by the number of shoots per meter square.

The data collection in the mixed community was a combination of the methods used in the pure communities. *Scirpus* was sampled by measuring individual stems, while *Spartina* and *Distichlis* were sampled as in *Spartina*. *Spartina* and *Distichlis* were measured separately. The mixed community was censused three times during the 1988 season.

Statistical analyses were done using a two way anova, correcting the effect of elevated CO_2 for block effect. A block consists of three chambers; elevated, ambient and control, which are close together and therefore expected to share the same specific site conditions.

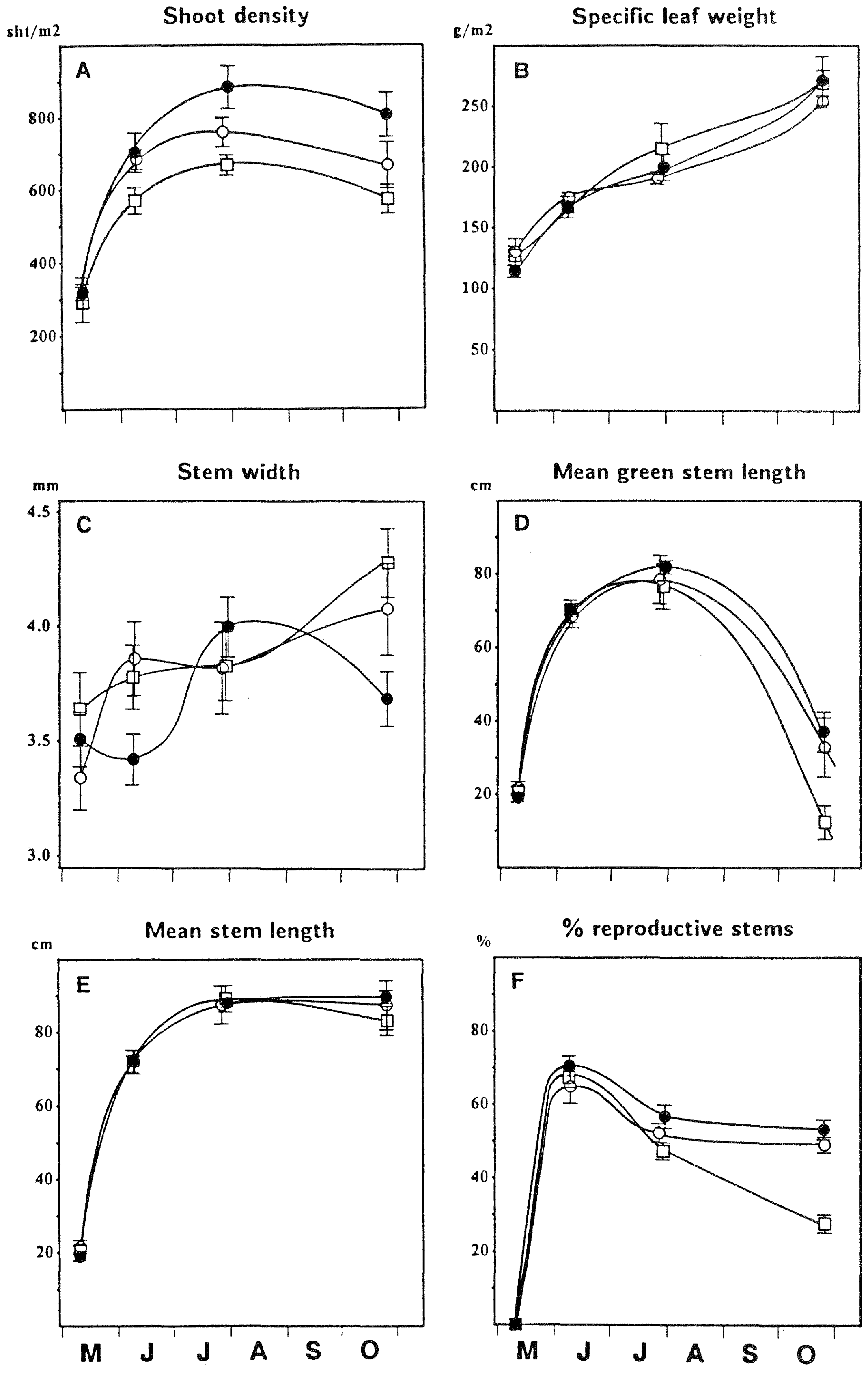
Results

Scirpus community

Figure 2.2 and table 2.1 show the effect of elevated CO_2 on the *Scirpus* community. Shoot density, total biomass and green biomass were higher in the elevated chambers at harvest 3 and 4, but only for shoot density were the elevated chambers significantly different from the ambient chambers. A significant chamber effect was found at the end of the season where percent senescence was higher in the control sites, while the green stem length and the percent reproductive stems were higher in the ambient and elevated chambers. No significant effect was found on mean total stem length and specific leaf weight.

Figure 2.3 shows shoot density for each treatment as a function of 10 cm shoot height classes for the four harvests. The increase in shoot density at elevated CO_2 was caused by a large increase in shoot density in only a few height classes.

Large differences existed between blocks as is shown in figure 2.4 and table 2.2. Biomass, shoot density and shoot height decreased from block 1 and 2 to block 5, while the reverse order was true for senescence. These data suggest that an environmental gradient in the *Scirpus* community is affecting growth. The block effect was corrected for treatment effect in the statistical analysis.



Shoot density

Specific leaf weight

Stem width

Mean green stem length

Mean stem length

% reproductive stems

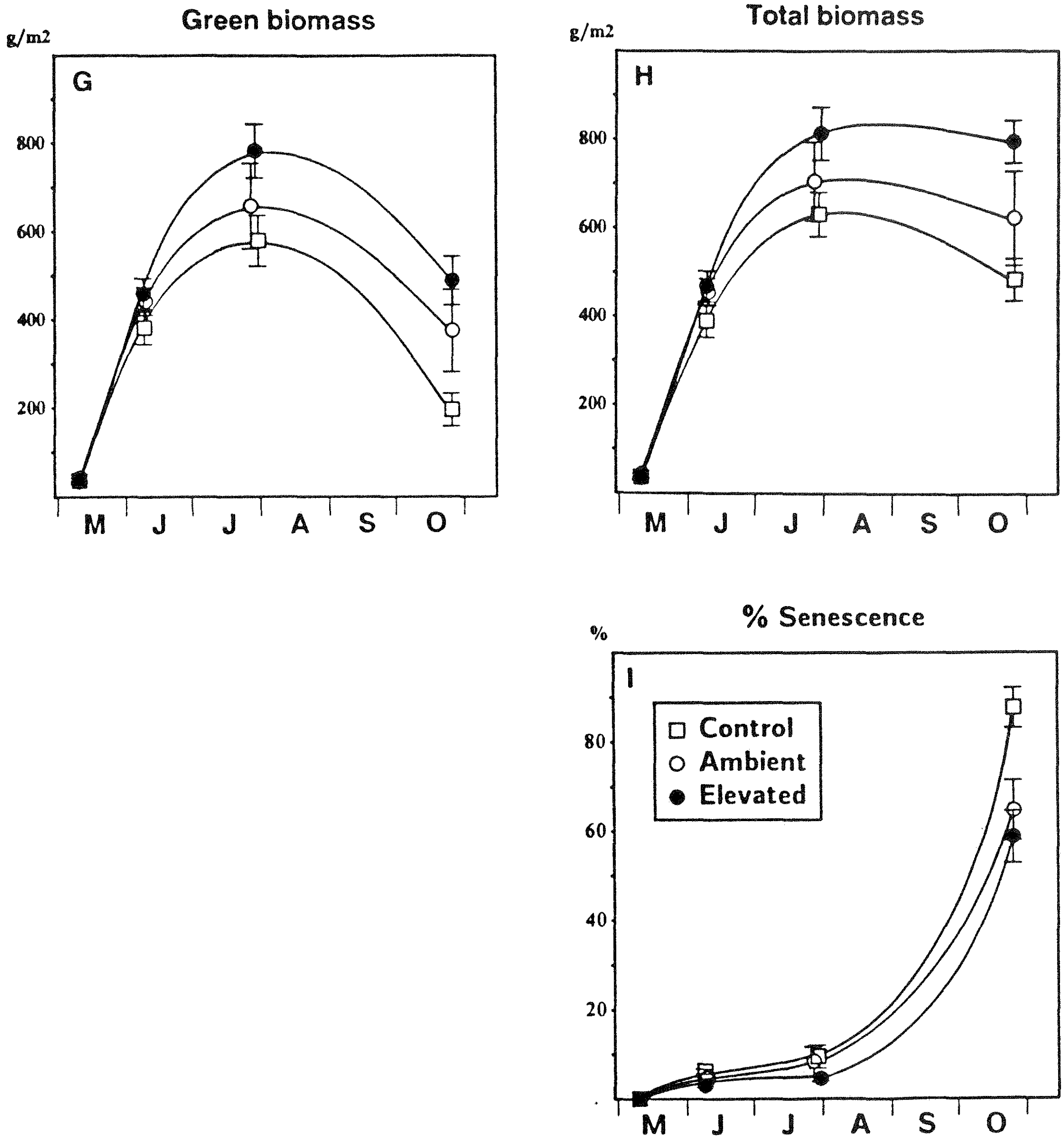


Figure 2.2. Harvest data for the *Scirpus* community. Mean and standard error of five chambers are shown for each harvest and treatment. A. shoot density; B. Specific leaf weight expressed as dry weight per unit area of one face of the Scirpus stem; C. Stem width of harvested shoots; D. Mean green shoot length; E. Mean total shoot length; F. Percentage of flowering shoots; G. Green (non-senescent) biomass; G. Total biomass.

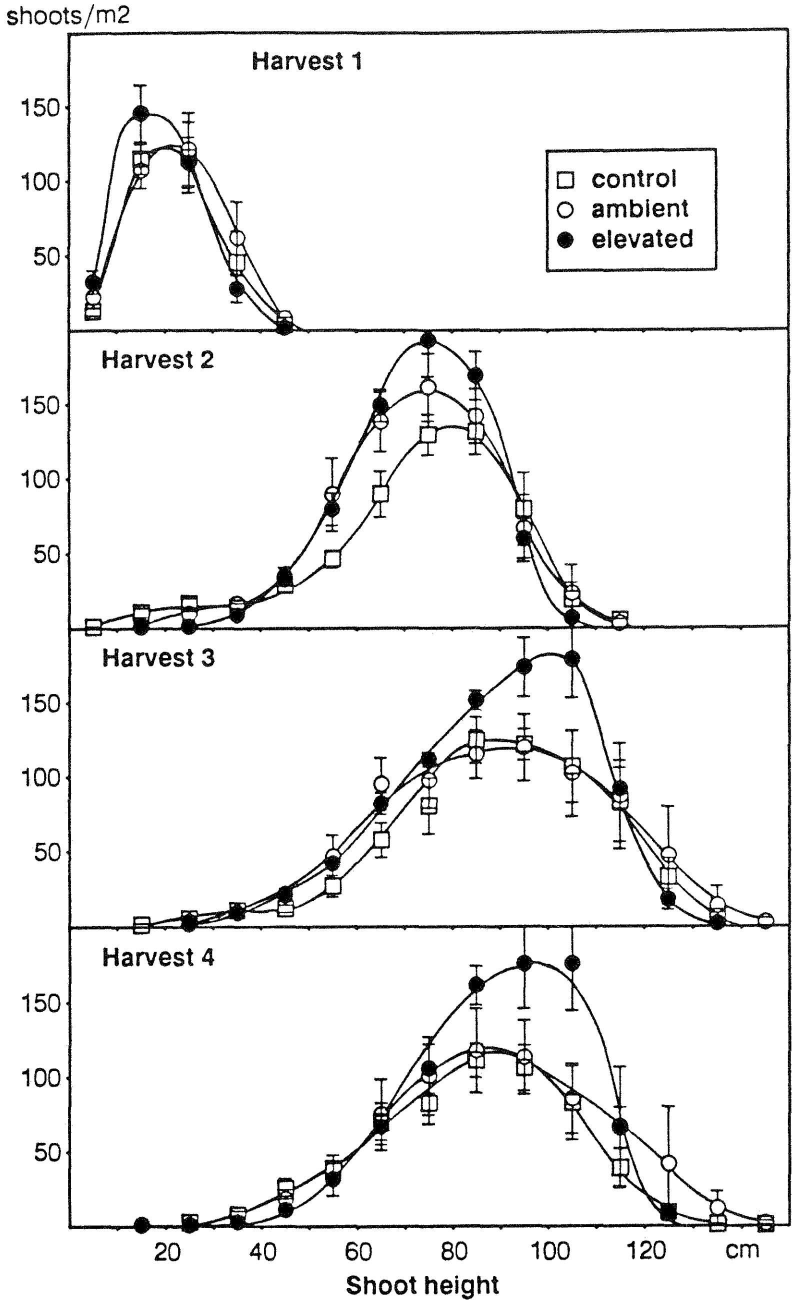


Figure 2.3. Number of *Scirpus* shoots in 10 cm height classes for the four 1988 harvests. Values are means and standard errors for five chambers.

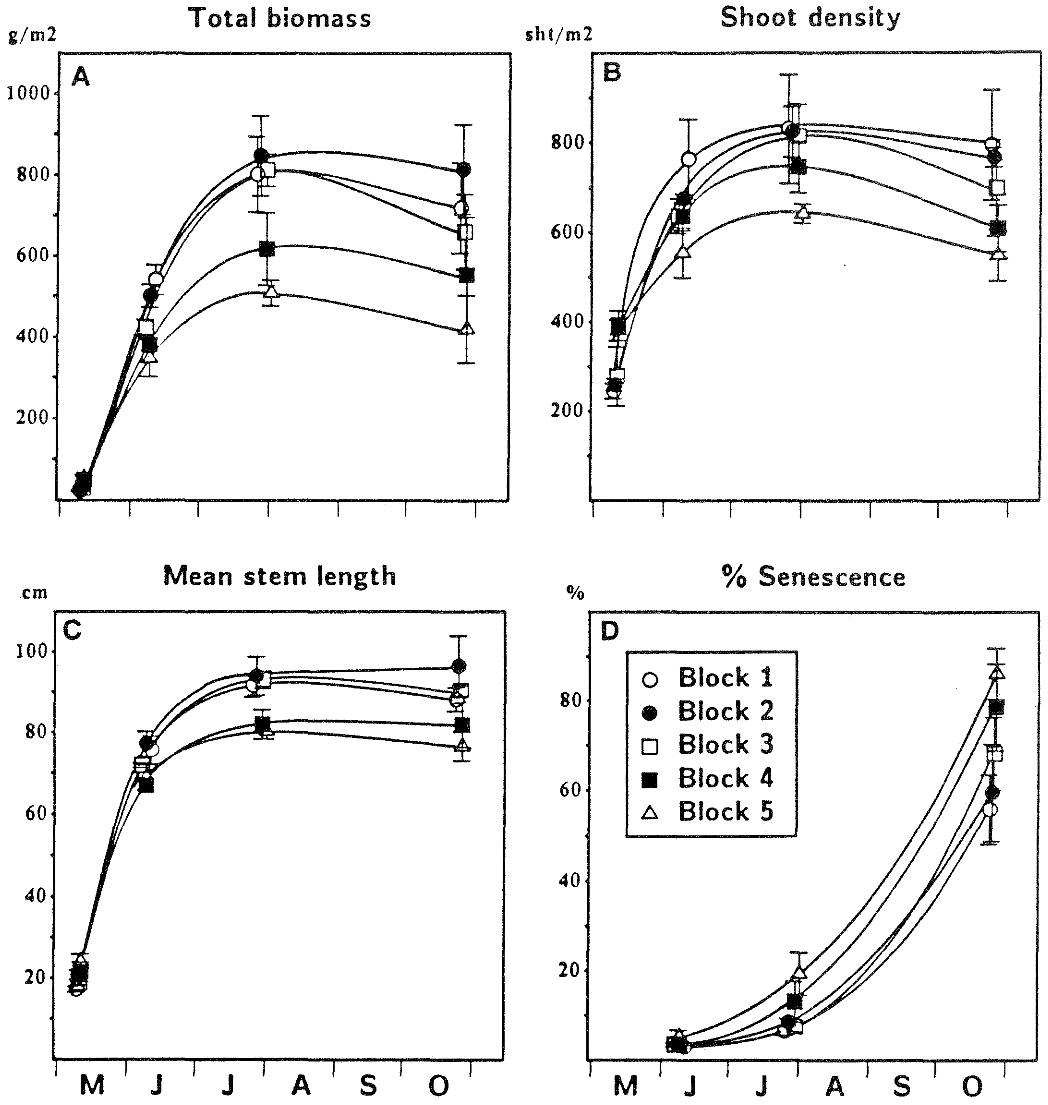
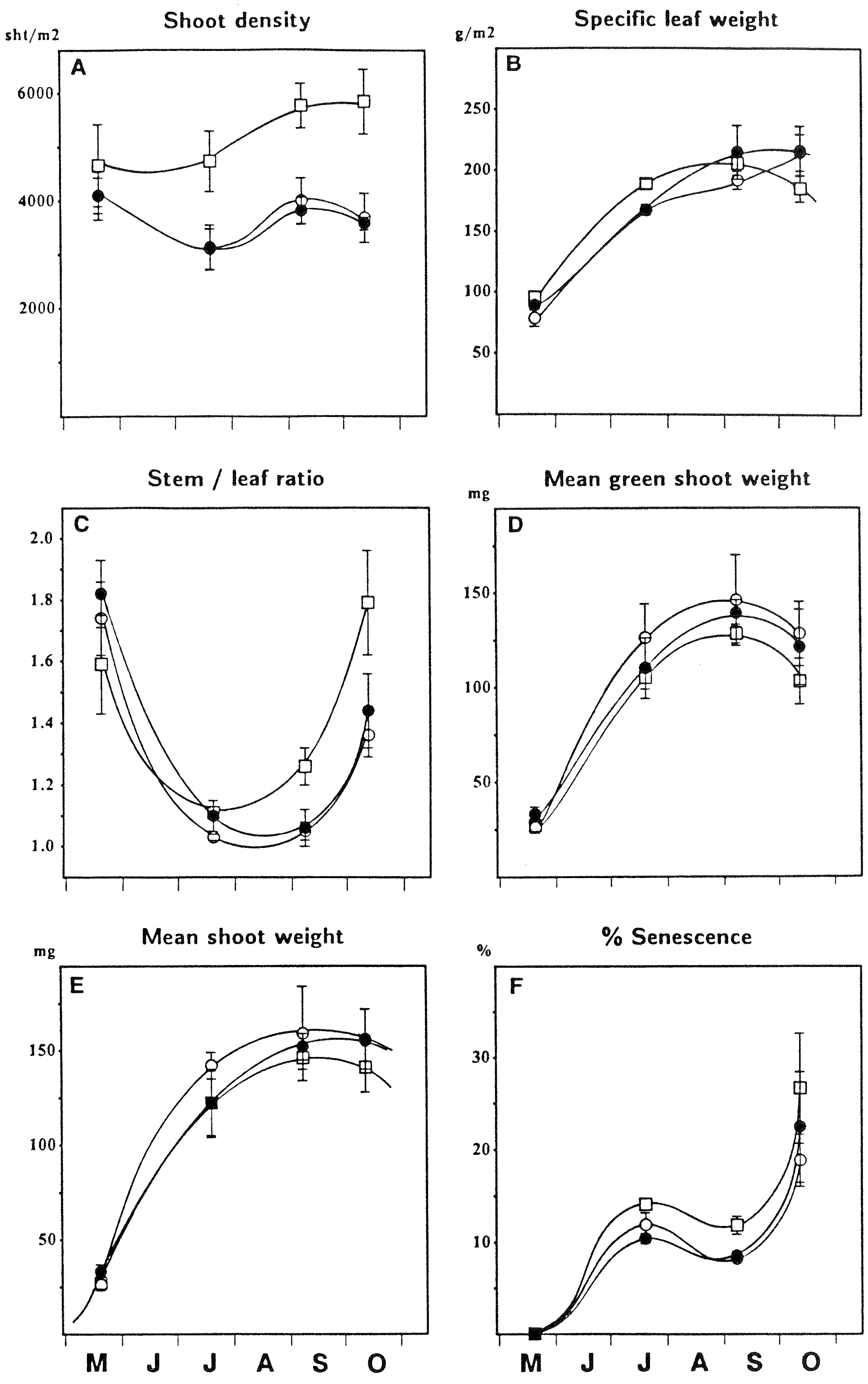


Figure 2.4. Effect of the location of the chambers within the *Scirpus* community on total biomass (A), shoot density (B), shoot length (C), and senescence (D) of *Scirpus*. Values are means and standard errors for three chambers (one block, consisting of one elevated chamber, one ambient chamber and one control site) for four harvests.



Shoot density

Specific leaf weight

Stem / leaf ratio

Mean green shoot weight

Mean shoot weight

% Senescence

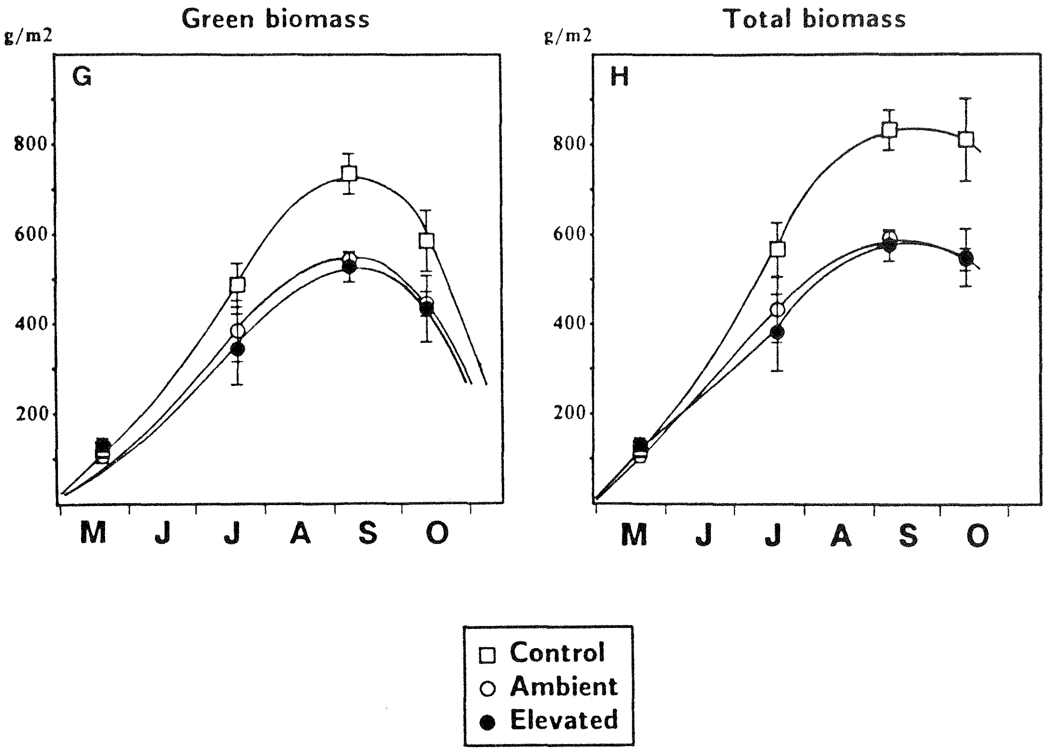


Figure 2.5. Harvest data for the *Spartina* community. Means and standard errors of five chambers are shown for each harvest and treatment. A. Shoot density; B. Specific leaf weight; C. Stem / leaf weight ratio; D. Green shoot weight; E. Total shoot weight; F. Percent senescence; G. Green (non senescent) biomass; H. Total biomass.

Spartina community

The growth analysis results for the *Spartina* community are presented in figure 2.5 and table 2.3. No significant differences were found between plants from elevated and ambient chambers, but there was a significant chamber effect. Control sites had a significantly higher shoot density by the second harvest and produced significantly more biomass than chambered sites by the third harvest. Plants in control sites also had a significantly higher senescence rate and were producing fewer leaves per unit biomass.

Mixed community

The mixed community is made up of a combination of the species *Scirpus olneyi*, *Spartina patens* and *Distichlis spicata*, but the distribution of these three species within the mixed community is not homogeneous (figure 2.6). *Scirpus* occupies a small but fairly constant percentage of the biomass, while the percentages for *Spartina* and *Distichlis* vary between 0 and 95 %.

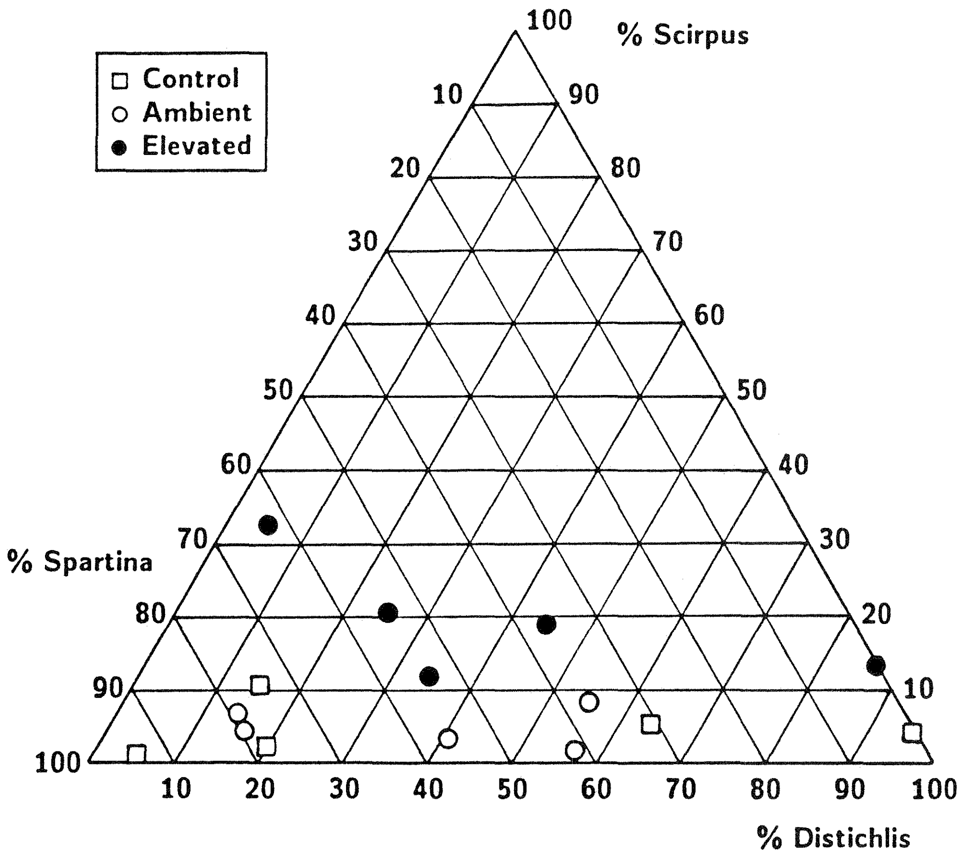
Elevated CO_2 had a very large effect on *Scirpus olneyi* in the mixed community (figure 2.7, table 2.4). There was a significant increase in shoot density, total and green biomass, and green stem length by the second harvest. Percent senescence was significantly lower in the elevated chambers at the last harvest.

Spartina patens growing in the mixed community showed no significant response to elevated CO_2, except for specific leaf weight at the final harvest (figure 2.8, table 2.5). There was a trend towards lower density and biomass in the elevated chambers. As in the pure community, a chamber effect was present delaying senescence and decreasing the stem/leaf ratio.

Shoot density and biomass of *Distichlis spicata* was higher in the elevated chambers than in the ambient chambers, but the effect was not significant due to the high variability in the data (figure 2.9, table 2.6). The percentage of reproductive stems was lower and senescence was higher in the control sites but this effect was not significant.

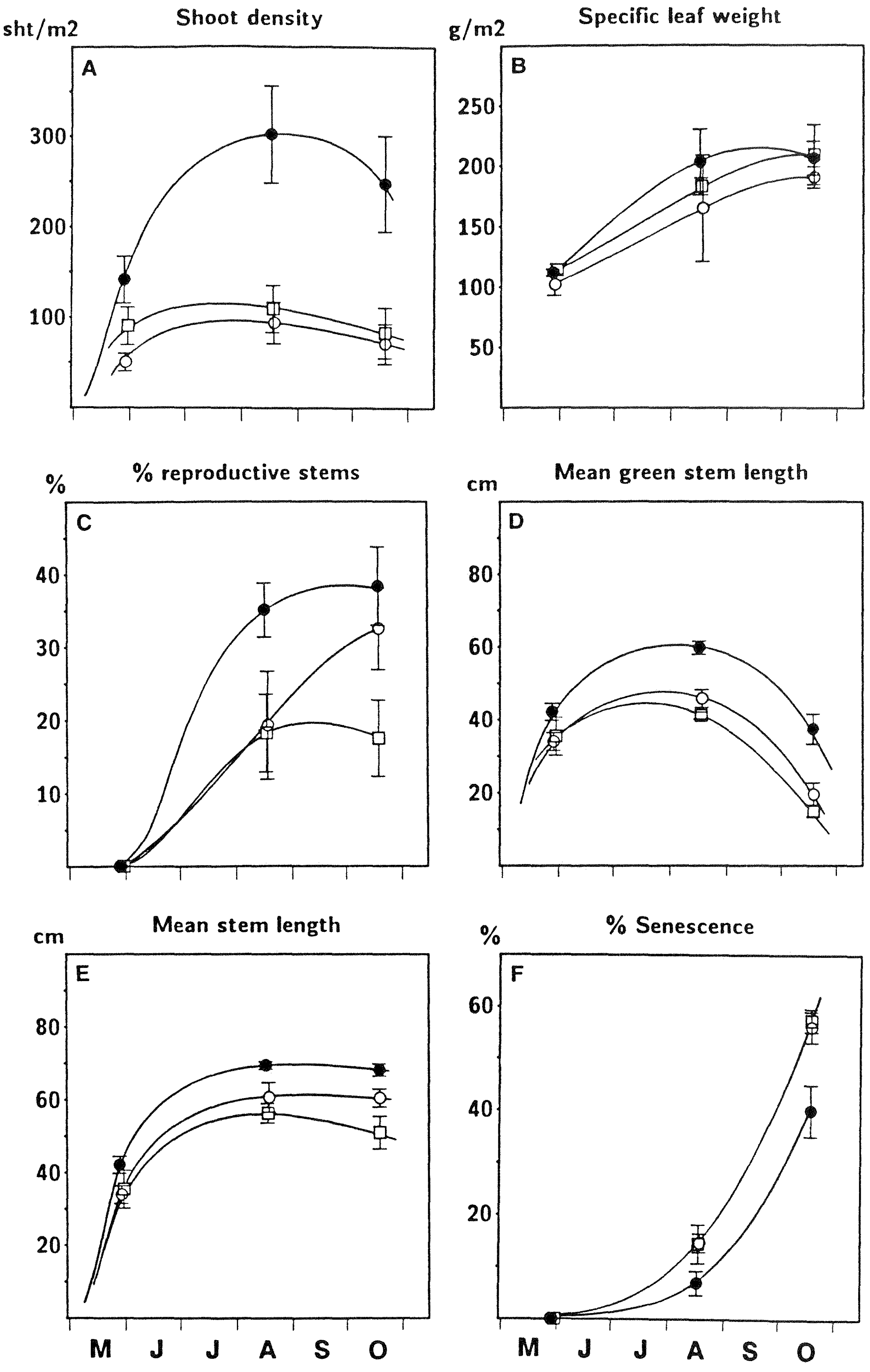
Scirpus olneyi represents only 2 to 33 % of the biomass in the mixed community, and the shoot density, stem height and percentage of reproductive stems were lower than in the pure *Scirpus* community. The relative effect of elevated CO_2 on *Scirpus* however was much larger in the mixed community than in the pure *Scirpus* community (figure 2.10). Density and green biomass increased by 17 and 19 % in the pure community, while in the mixed community they increased by 222 and 354 %.

Scirpus biomass was significantly higher in the elevated chambers, both in absolute and in relative amounts. Although neither *Spartina* nor *Distichlis* showed a significant decline, the data suggest that the relative standing of *Distichlis* was not changed in elevated CO_2, and that the relative increase in *Scirpus* was at the expense of *Spartina* (figure 2.11).



Species composition in chambers of the mixed community.

Figure 2.6. Species composition in chambers of the mixed community. The position in the graph is based on the percentage of the total biomass in the chamber of each of the three species.


sht/m2
Shoot density
A
300
200
100
g/m2
Specific leaf weight
B
250
200
150
100
50
%
% reproductive stems
C
40
30
20
10
cm
Mean green stem length
D
80
60
40
20
cm
Mean stem length
E
80
60
40
20
%
% Senescence
F
60
40
20
M
J
J
A
S
O
M
J
J
A
S
O

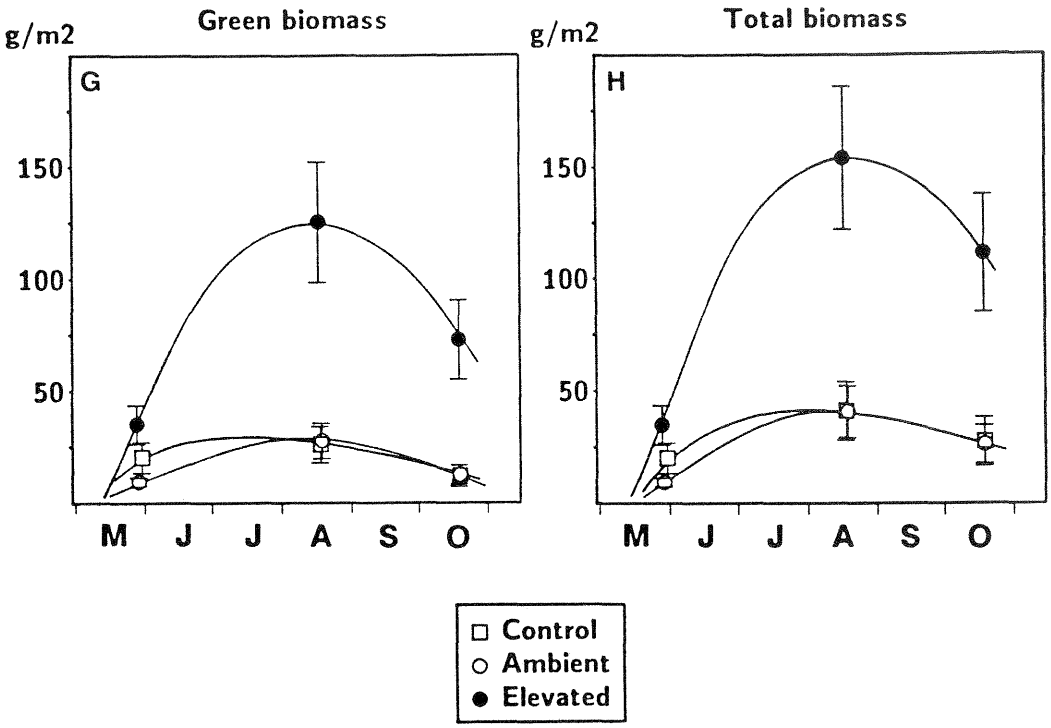
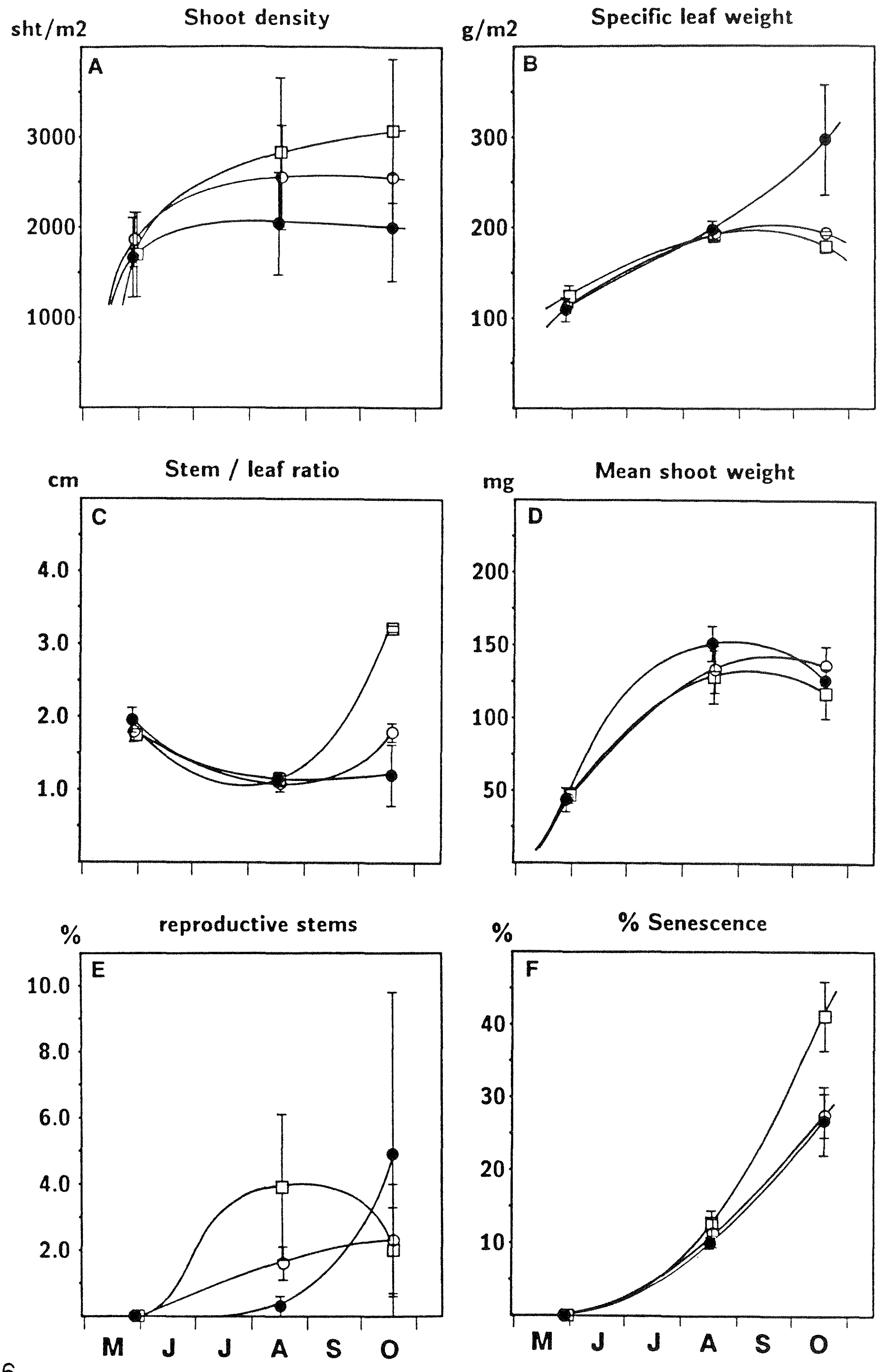


Figure 2.7. Harvest data for *Scirpus olneyi* in the mixed community. Mean and standard error of five chambers are shown for each harvest and treatment. A. Shoot density; B. Specific leaf weight; C. Percentage of flowering shoots; D. Green shoot length; E. Total shoot length; F. Percent senescence (on shoot length basis); G. Green (non senescent) biomass; H. Total biomass.


Shoot density
sht/m2
A
3000
2000
1000
Specific leaf weight
g/m2
B
300
200
100
Stem / leaf ratio
cm
C
4.0
3.0
2.0
1.0
Mean shoot weight
mg
D
200
150
100
50
reproductive stems
%
E
10.0
8.0
6.0
4.0
2.0
% Senescence
%
F
40
30
20
10
M J J A S O
M J J A S O

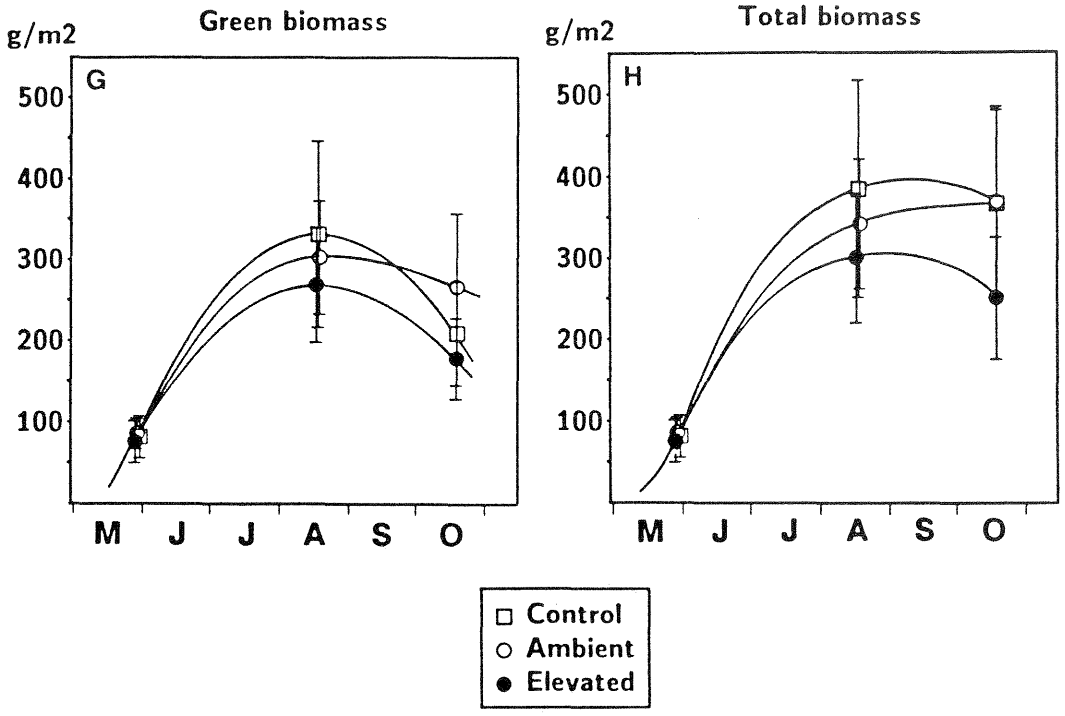
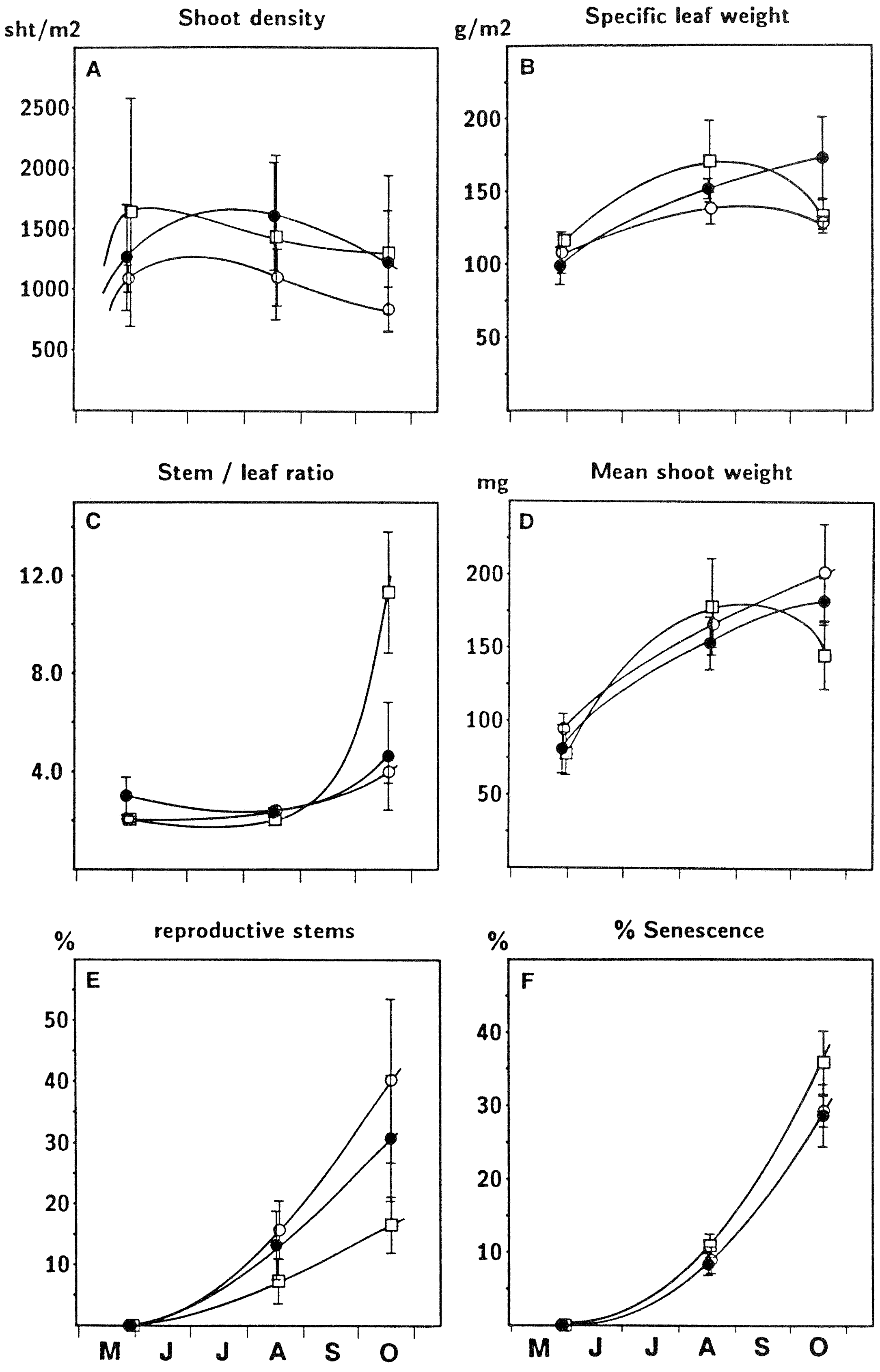


Figure 2.8. Harvest data for *Spartina patens* in the Mixed community. Mean and standard error of five chambers are shown for each harvest and treatment. A. Shoot density; B. Specific leaf weight; C. Stem / leaf weight ratio; D. Green shoot weight; E. Total shoot weight; F. Percent senescence; G. Green (non senescent) biomass; H. Total biomass.


Shoot density
sht/m2
A
2500
2000
1500
1000
500
Specific leaf weight
g/m2
B
200
150
100
50
Stem / leaf ratio
C
12.0
8.0
4.0
Mean shoot weight
mg
D
200
150
100
50
reproductive stems
%
E
50
40
30
20
10
M
J
J
A
S
O
% Senescence
%
F
40
30
20
10
M
J
J
A
S
O

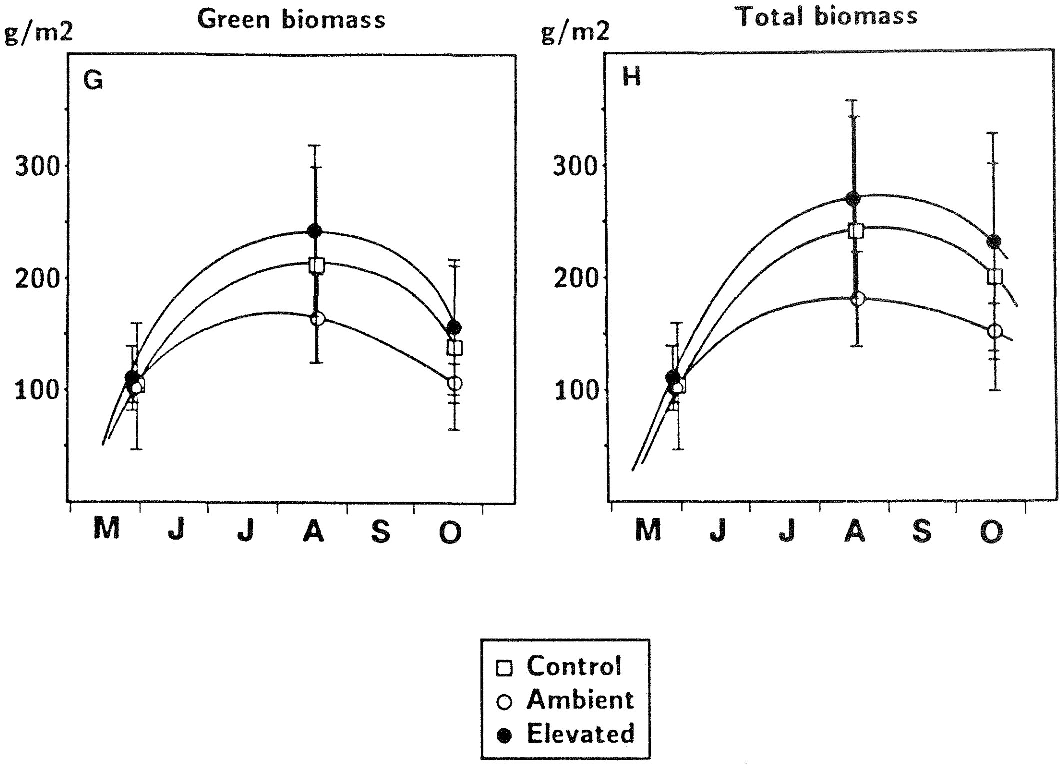


Figure 2.9. Harvest data for *Distichlis spicata* in the Mixed community. Mean and standard error of five chambers are shown for each harvest and treatment. A. Shoot density; B. Specific leaf weight; C. Stem / leaf weight ratio; D. Green shoot weight; E. Total shoot weight; F. Percent senescence; G. Green (non senescent) biomass; H. Total biomass.

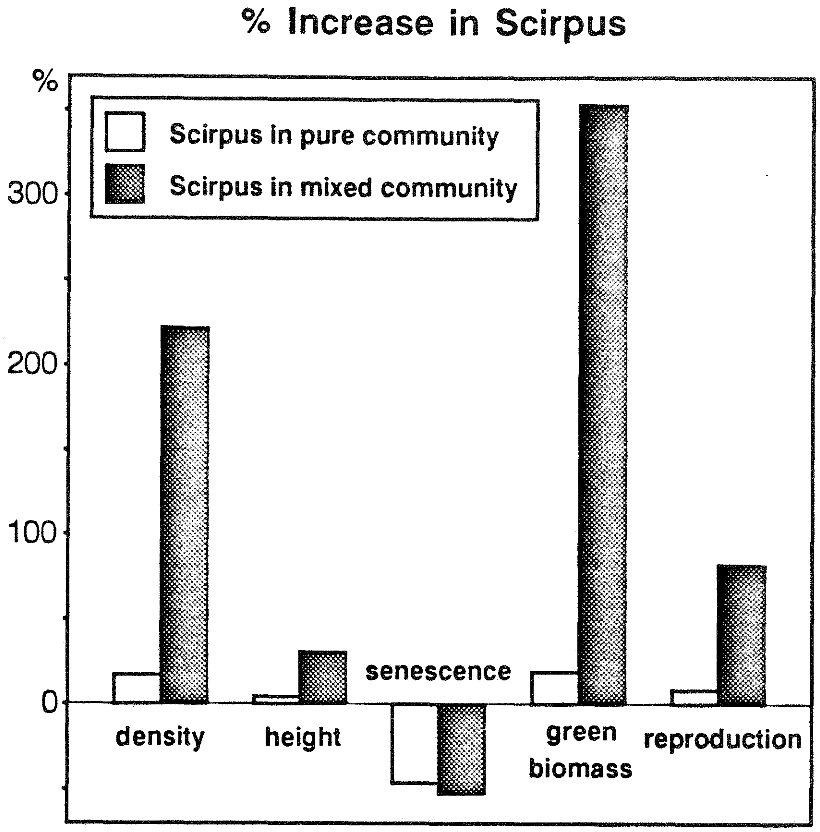


Figure 2.10. A comparison of the effects of elevated CO_2 on *Scirpus olneyi* growing in the mixed and in the C_3 community. The percent increase in shoot density, shoot height, percent senescence, green biomass and reproduction is shown of plants grown in elevated CO_2 as compared with plants grown in ambient CO_2.

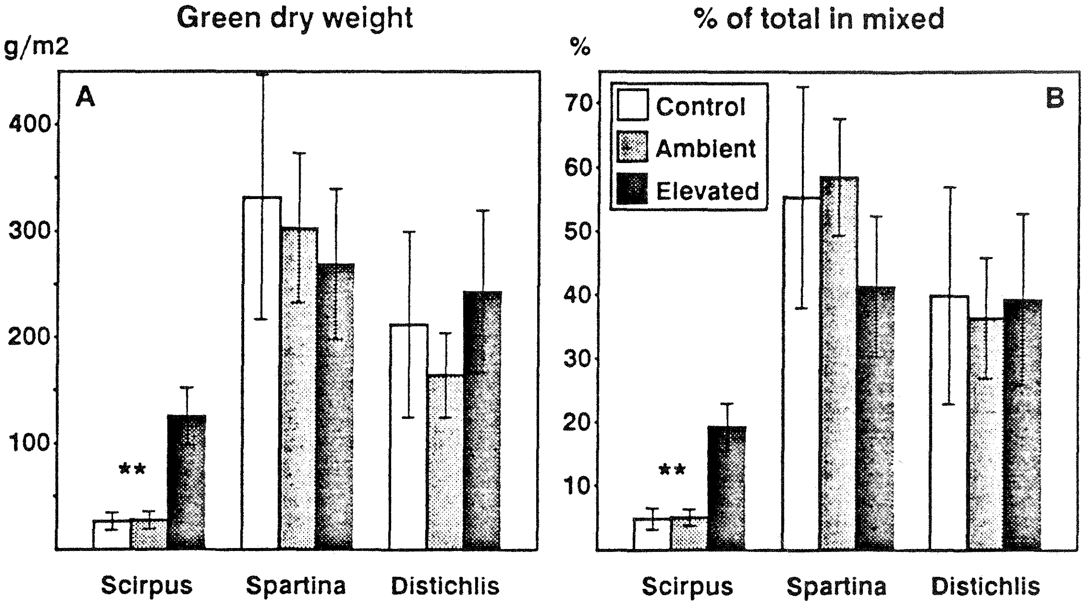


Figure 2.11. A comparison of the biomass of the three species in the mixed community at peak standing biomass. A] The absolute amount of biomass for each of the species, B] The percentage of the total biomass. Values shown are means and standard errors of five chambers.

Belowground biomass.

Methods.

In order to estimate the belowground biomass of vegetation in the chambers, root cores of ca. 5 cm diameter and 20 cm deep were collected in chambers and control sites. The substrate of the marsh consists almost completely of organic material, making it very difficult to discriminate between the living roots and the substrate. To facilitate this, cores of marsh substrate were replaced with sifted peat moss before the start of the 1988 growing season. Roots and rhizomes were allowed to grow into these cores during the season. These regrowth cores were then harvested at the end of the growing season.

Both original cores and regrowth cores were cut into 5 cm sections. From the original cores living rhizomes were isolated as well as a fraction of non rhizome material larger than 2 mm. In regrowth cores it was possible to identify both rhizomes and roots, although it was not possible to differentiate between roots from the three species in the mixed community. Rhizomes from *Scirpus* could be distinguished from *Spartina* and *Distichlis* rhizomes. Dry weight of roots and rhizomes was measured for each section.

Results.

Figure 2.12 and table 2.7 show the root and rhizome biomass in the regrowth cores of the *Scirpus* community. Elevated CO_2 had a large effect on the root biomass of Scirpus, increasing the root biomass by an average of 57 percent. Root biomass was evenly distributed over the four sections, suggesting that a considerable amount of root biomass may be present below 20 cm. No significant effect of elevated CO_2 was found on *Scirpus* rhizomes. The largest density of rhizomes was found between 5 and 15 cm below the surface.

Elevated CO_2 had no significant effect on root and rhizome biomass in the regrowth cores of the *Spartina* community (figure 2.13, table 2.7). The majority of the *Spartina* rhizomes were found in the top 5 cm, while the roots were concentrated in the first 10 cm. Almost no roots or rhizomes were found below 15 cm.

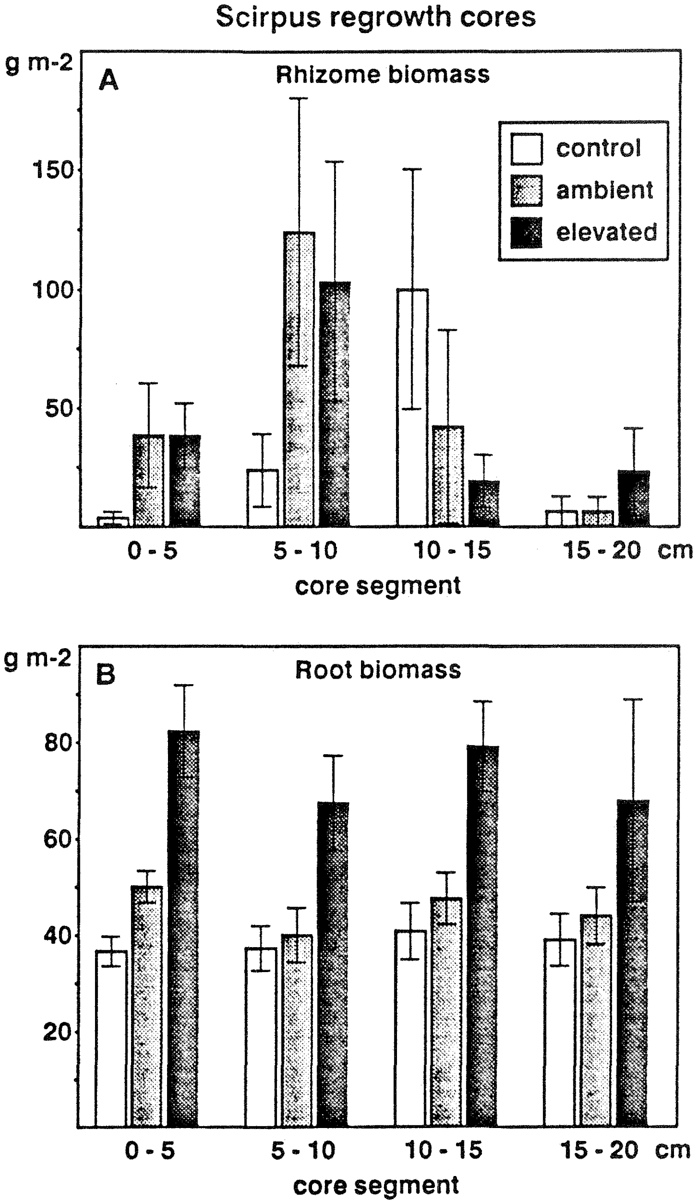


Figure 2.12. Biomass of rhizomes (A) and roots (B) in regrowth cores of the Scirpus community. Values are means and standard errors.

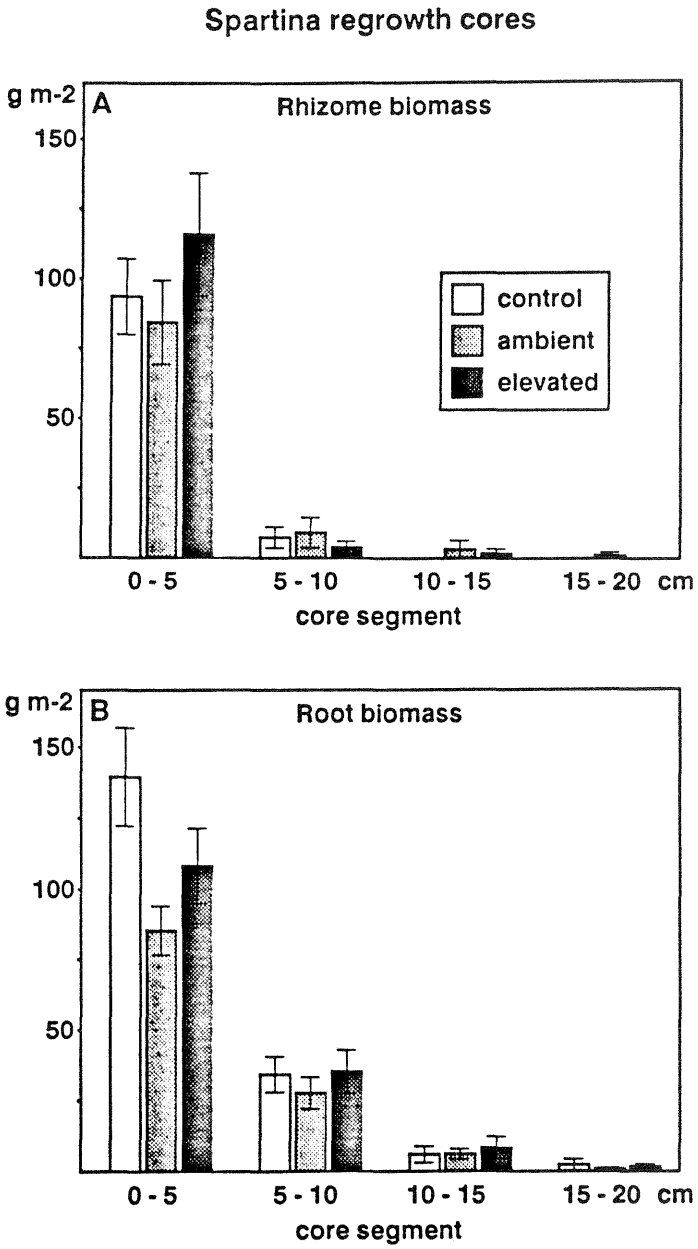


Figure 2.13. Belowground biomass in regrowth cores of the *Spartina* community. A. Rhizomes, B. Roots.

In the mixed community it was not possible to separate roots by species. The vertical distribution of *Scirpus* and *Spartina* roots in the mixed community appeared to follow the same pattern as in the pure communities, with the C_4 species providing most of the biomass and occupying the top core segments, and *Scirpus* being distributed evenly over the core segments (fig. 2.14). The highest density of roots was found in the first core segment (0 to 5 cm), and no effect of elevated CO_2 was found in this segment. In the lowest two segments (10 to 20 cm) where *Scirpus* roots are likely to dominate, a significant CO_2 effect was found. The 5 to 10 cm segment shows an intermediate pattern.

It was possible to distinguish between C_3 and C_4 rhizomes in the cores from the mixed community. The distribution of C_4 rhizomes follows the same pattern as *Spartina* rhizomes in the pure community and there was no effect of elevated CO_2. In order to minimize disturbance in the study sites, only a few cores with a small diameter were taken from each site. This gives good results with the C_4 rhizomes which are thin and form a dense mat. The *Scirpus* rhizomes however are thick and sparse, causing a very large variability in the biomass data for *Scirpus* rhizomes. Due to this high variability there were no significant treatment effects on rhizome biomass in the original root cores (figure 2.15, table 2.8). The data show that the rhizome biomass in the original cores was six (*Spartina*) to twelve (*Scirpus*) times higher than the rhizome biomass in the regrowth cores. The fraction with material larger than 2 mm includes roots, but also other material, making it impossible to draw any conclusions regarding the effect of elevated CO_2 on the root mass in the original root zone of these perennial communities.

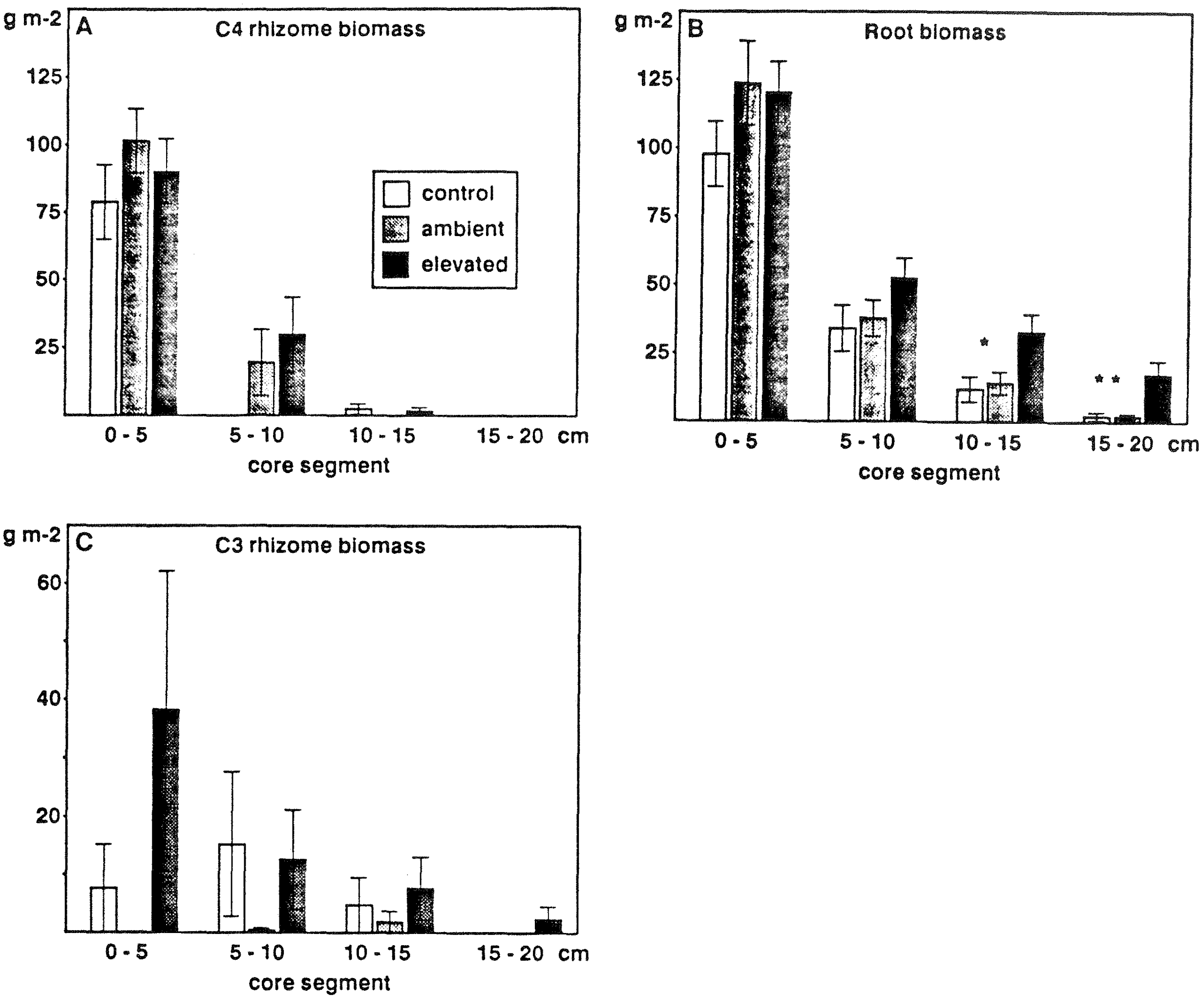


Figure 2.14. Belowground biomass in regrowth cores of the mixed community. A. C_4 rhizomes, B. All roots, C. C_3 rhizomes.

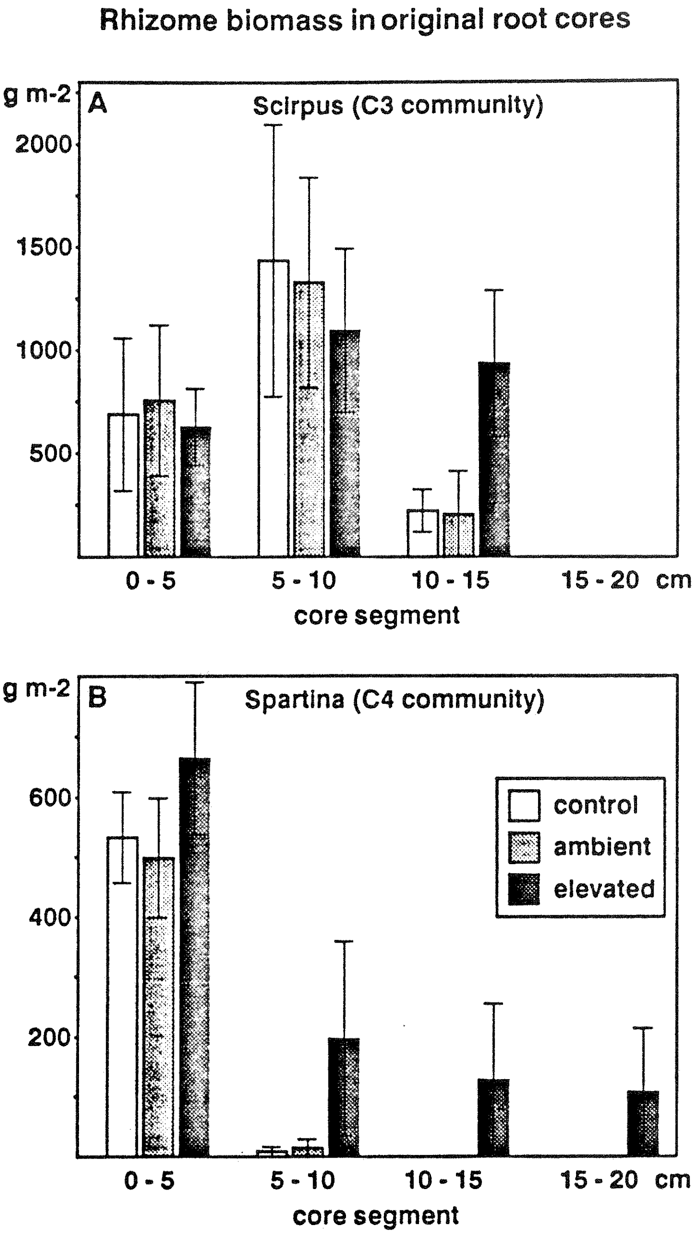


Figure 2.15. Rhizome biomass of *Scirpus* (C_3 community) and *Spartina* (C_4 community) in original root cores. Mean and standard error of four root cores. A. *Scirpus*, B. *Spartina*.

Table 2.1. Harvest data for *Scirpus olneyi* in the C_3 community. Mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1			Harvest 2			Harvest 3			Harvest 4		
Julian day	131.5			160.8			210.9			300.0		
Shoot density (shoots m-2)												
control	291	(52)	a	570	(36)	a	668	(28)	a	573	(39)	a
ambient	320	(42)	a	684	(28)	b	758	(40)	a	666	(64)	a
elevated	318	(18)	a	703	(54)	b	884	(60)	b	807	(62)	b
		p = 0.75			p = 0.167			p = 0.016			p = 0.037	
Total biomass (g m-2)												
control	35.9	(8.76)	a	390.4	(41.9)	a	631.6	(60.0)	a	484.3	(53.4)	a
ambient	41.6	(9.50)	a	454.7	(34.8)	a	705.7	(99.2)	a	622.8	(118)	b
elevated	33.3	(2.86)	a	468.2	(39.4)	a	813.7	(51.5)	a	794.3	(56.8)	b
		p = 0.66			p = 0.53			p = 0.66			p = 0.106	
Green biomass (g m-2)												
control	35.9	(8.76)	a	382.7	(41.7)	a	580.5	(64.7)	a	195.8	(41.2)	a
ambient	41.6	(9.50)	a	442.7	(35.4)	a	659.1	(108)	b	375.8	(104)	b
elevated	33.3	(2.86)	a	460.3	(39.1)	a	783.1	(68.2)	b	490.0	(61.3)	b
		p = 0.66			p = 0.29			p = 0.058			p = 0.0063	
Total stem length (cm)												
control	20.8	(1.2)	a	72.2	(3.0)	a	89.2	(3.6)	a	83.1	(3.9)	a
ambient	21.5	(1.9)	a	71.9	(3.2)	a	87.5	(5.2)	a	87.4	(6.7)	a
elevated	19.0	(1.2)	a	72.3	(1.3)	a	87.9	(1.1)	a	89.6	(1.8)	a
		p = 0.33			p = 0.99			p = 0.90			p = 0.49	
Green stem length (cm)												
control	20.8	(1.2)	a	69.7	(3.1)	a	76.4	(6.2)	a	12.4	(4.6)	b
ambient	21.5	(1.9)	a	68.6	(3.3)	a	78.4	(6.6)	a	32.8	(8.1)	a
elevated	19.0	(1.2)	a	70.2	(1.3)	a	81.8	(1.8)	a	37.1	(5.4)	a
		p = 0.33			p = 0.88			p = 0.58			p = 0.001	
reproductive stems (%)												
control	0	(0)	a	67.3	(2.7)	a	47.2	(2.3)	a	27.5	(2.4)	b
ambient	0	(0)	a	64.8	(4.6)	a	52.2	(2.6)	ab	48.9	(2.1)	a
elevated	0	(0)	a	70.5	(2.8)	a	56.6	(3.2)	b	53.0	(2.7)	a
					p = 0.48			p = 0.09			p = 0.0002	
% Senescence (% dry weight)												
control	0	(0)	a	6.1	(0.55)	ab	9.4	(2.6)	a	87.6	(4.5)	b
ambient	0	(0)	a	4.6	(1.00)	a	8.3	(3.3)	a	64.6	(6.8)	a
elevated	0	(0)	a	2.9	(0.46)	b	4.5	(0.6)	a	58.7	(5.9)	a
					p = 0.10			p = 0.15			p = 0.0001	
Specific leaf weight (g m-2)												
control	127	(8)	a	167	(9)	a	215	(21)	a	269	(11)	a
ambient	130	(11)	a	175	(4)	a	191	(5)	a	254	(5)	a
elevated	114	(5)	a	166	(4)	a	200	(11)	a	271	(20)	a
		p = 0.63			p = 0.52			p = 0.14			p = 0.58	

Table 2.2. Harvest data for *Scirpus olneyi* in the C_3 community. Mean and standard error for each block of three chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1			Harvest 2			Harvest 3			Harvest 4		
Julian day	131.5			160.8			210.9			300.0		
Shoot density (shoots m-2)												
block 1	243	(17)	a	763	(89)	a	829	(122)	a	793	(122)	a
block 2	258	(14)	ab	675	(10)	ab	823	(56)	a	765	(21)	ab
block 3	277	(66)	abc	635	(38)	bc	813	(71)	a	697	(108)	abc
block 4	391	(33)	c	635	(30)	bc	745	(58)	ab	607	(52)	bc
block 5	380	(23)	bc	553	(56)	c	641	(21)	b	547	(57)	c
		p = 0.072			p = 0.029			p = 0.060			p = 0.037	
Total biomass (g m-2)												
block 1	22.4	(1.7)	a	540	(37)	a	801	(93)	ab	719	(111)	ab
block 2	30.2	(3.6)	ab	500	(28)	a	847	(98)	a	814	(110)	a
block 3	28.5	(6.5)	ab	422	(20)	b	812	(40)	ab	660	(92)	abc
block 4	49.1	(10.1)	bc	380	(14)	b	617	(91)	bc	555	(143)	bc
block 5	54.3	(8.2)	c	347	(46)	b	509	(32)	c	420	(83)	c
		p = 0.049			p = 0.0022			p = 0.023			p = 0.041	
Green biomass (g m-2)												
block 1	22.4	(1.7)	a	531	(38)	a	774	(94)	ab	459	(103)	a
block 2	30.2	(3.6)	ab	490	(27)	a	809	(99)	a	513	(130)	a
block 3	28.5	(6.5)	ab	413	(19)	b	779	(40)	ab	363	(84)	ab
block 4	49.1	(10.1)	bc	372	(14)	bc	573	(100)	bc	271	(118)	bc
block 5	54.3	(8.2)	c	336	(45)	c	437	(52)	c	163	(54)	c
		p = 0.049			p = 0.0023			p = 0.034			p = 0.0063	
Total stem length (cm)												
block 1	17.23	(0.7)	a	75.64	(3.4)	ab	91.71	(2.9)	a	88.23	(2.9)	ab
block 2	20.76	(1.2)	ab	77.23	(3.1)	a	93.99	(4.8)	a	96.46	(7.5)	a
block 3	18.75	(0.4)	a	71.91	(0.6)	ab	93.13	(2.3)	a	90.39	(1.3)	a
block 4	21.46	(2.5)	ab	66.94	(1.3)	b	81.92	(3.6)	ab	81.9	(5.4)	bc
block 5	24.02	(1.9)	b	68.94	(3.1)	ab	80.37	(2.0)	b	76.57	(3.5)	c
		p = 0.085			p = 0.136			p = 0.030			p = 0.0032	
% Senescence (dry weight)												
block 1	0.0	(0.0)		2.9	(0.3)	a	6.50	(1.0)	a	55.8	(7.6)	a
block 2	0.0	(0.0)		3.57	(0.2)	ab	8.45	(0.9)	a	59.6	(10.8)	a
block 3	0.0	(0.0)		3.32	(0.4)	ab	7.52	(1.0)	a	68.2	(8.1)	b
block 4	0.0	(0.0)		3.53	(0.4)	ab	13.0	(4.6)	ab	78.5	(9.8)	c
block 5	0.0	(0.0)		5.14	(1.4)	b	19.33	(4.8)	b	86.1	(5.7)	c
					p = 0.19			p = 0.020			p = 0.0001	

Table 2.3. Harvest data for *Spartina patens* in the C_4 community. Mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1			Harvest 2			Harvest 3			Harvest 4		
Julian day	141.0			201.6			251.5			286.2		
Shoot density (shoots m-2)												
control	4652	(767)	a	4720	(561)	b	5752	(414)	b	5844	(602)	b
ambient	4088	(334)	a	3112	(416)	a	3990	(429)	a	3672	(463)	a
elevated	4084	(449)	a	3084	(379)	a	3804	(255)	a	3560	(126)	a
		p = 0.70			p = 0.01			p = 0.008			p = 0.005	
Total biomass (g m-2)												
control	122.0	(20.1)	a	567.1	(59.4)	a	831.4	(44.7)	b	809.7	(91.8)	b
ambient	105.5	(15.3)	a	432.5	(73.2)	ab	591.7	(16.2)	a	545.6	(24.0)	a
elevated	130.8	(16.4)	a	381.3	(85.9)	b	576.0	(35.4)	a	549.8	(64.3)	a
		p = 0.24			p = 0.04			p = 0.001			p = 0.04	
Green biomass (g m-2)												
control	122.0	(20.1)	a	486.6	(49.3)	ab	734.4	(44.2)	b	585.3	(67.6)	a
ambient	105.5	(15.3)	a	383.0	(68.0)	a	543.6	(16.5)	a	443.9	(27.8)	a
elevated	130.8	(16.4)	a	342.6	(79.1)	b	527.5	(34.3)	a	433.3	(74.9)	a
		p = 0.24			p = 0.10			p = 0.004			p = 0.30	
Total shoot weight (mg shoot-1)												
control	27	(3)	a	122	(18)	a	146	(6)	a	141	(13)	a
ambient	26	(3)	a	142	(7)	a	159	(25)	a	156	(16)	a
elevated	33	(4)	a	122	(17)	a	152	(7)	a	155	(17)	a
		p = 0.17			p = 0.52			p = 0.85			p = 0.79	
Green shoot weight (mg shoot-1)												
control	27	(3)	a	105	(6)	a	128	(5)	a	103	(12)	a
ambient	26	(3)	a	126	(18)	a	146	(24)	a	128	(17)	a
elevated	33	(4)	a	110	(16)	a	139	(7)	a	121	(20)	a
		p = 0.17			p = 0.51			p = 0.72			p = 0.57	
Stem / leaf ratio (dry weight)												
control	1.59	(0.16)	a	1.11	(0.02)	a	1.26	(0.06)	b	1.79	(0.17)	b
ambient	1.74	(0.12)	a	1.03	(0.01)	a	1.05	(0.03)	a	1.36	(0.07)	a
elevated	1.82	(0.11)	a	1.10	(0.05)	a	1.06	(0.06)	a	1.44	(0.12)	a
		p = 0.15			p = 0.19			p = 0.02			p = 0.01	
% Senescence (dry weight)												
control	0	(0)	a	14.1	(0.65)	a	11.8	(0.97)	b	26.6	(6.0)	a
ambient	0	(0)	a	11.9	(1.34)	ab	8.2	(0.39)	a	18.8	(2.8)	a
elevated	0	(0)	a	10.4	(0.54)	b	8.5	(0.53)	a	22.4	(6.0)	a
					p = 0.04			p = 0.002			p = 0.50	
Specific leaf weight (g m-2)												
control	95.3	(5.5)	a	188.4	(3.8)	b	205.4	(9.7)	a	185.0	(10.8)	a
ambient	78.3	(6.6)	a	166.8	(2.7)	a	191.7	(7.3)	a	214.3	(15.1)	a
elevated	89.0	(3.1)	a	167.2	(4.6)	a	214.6	(22.1)	a	215.5	(20.3)	a
		p = 0.17			p = 0.001			p = 0.55			p = 0.19	

Table 2.4. Harvest data for *Scirpus olneyi* in the mixed community. Mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1			Harvest 2			Harvest 3		
Julian day	150.0			230.5			292.7		
Shoot density (shoots m-2)									
control	90	(21)	ab	109	(26)	a	83	(28)	a
ambient	50	(10)	a	94	(23)	a	71	(22)	a
elevated	141	(26)	e	302	(54)	b	248	(53)	b
		p = 0.02			p = 0.002			p = 0.006	
Total biomass (g m-2)									
control	20.2	(6.9)	ab	41.2	(13.0)	a	27.6	(10.8)	a
ambient	9.3	(2.0)	a	40.8	(11.4)	a	26.3	(8.6)	a
elevated	34.8	(8.8)	b	153.9	(31.9)	b	111.3	(26.3)	b
		p = 0.04			p = 0.003			p = 0.005	
Green biomass (g m-2)									
control	20.2	(6.9)	ab	25.9	(8.1)	a	12.0	(5.0)	a
ambient	9.3	(2.0)	a	27.6	(7.9)	a	12.5	(4.2)	a
elevated	34.8	(8.8)	b	125.3	(26.8)	b	72.8	(17.6)	b
		p = 0.04			p = 0.002			p = 0.003	
Total stem length (cm)									
control	35.4	(5.2)	a	56.2	(2.7)	a	50.9	(4.5)	a
ambient	33.9	(2.4)	a	60.6	(4.0)	ab	60.4	(2.4)	ab
elevated	42.1	(2.3)	a	69.3	(1.1)	b	68.0	(1.7)	b
		p = 0.25			p = 0.04			p = 0.02	
Green stem length (cm)									
control	35.4	(5.2)	a	41.1	(1.0)	a	14.9	(1.7)	a
ambient	33.9	(2.4)	a	45.8	(2.5)	a	19.5	(3.2)	a
elevated	42.1	(2.3)	a	59.7	(1.8)	b	37.4	(4.2)	b
		p = 0.25			p = 0.0002			p = 0.0007	
reproductive stems (%)									
control	0	(0)	a	18.2	(5.3)	a	17.5	(5.2)	a
ambient	0	(0)	a	19.3	(7.4)	a	32.5	(5.6)	b
elevated	0	(0)	a	35.1	(3.7)	a	38.3	(5.4)	b
					p = 0.13			p = 0.003	
% Senescence (% dry weight)									
control	0	(0)	a	14.4	(3.7)	a	57.4	(2.2)	a
ambient	0	(0)	a	14.6	(1.8)	a	56.1	(3.0)	a
elevated	0	(0)	a	6.9	(2.3)	a	40.0	(4.9)	b
					p = 0.10			p = 0.004	
Specific leaf weight (g m-2)									
control	114	(5)	a	183	(7)	a	209	(25)	a
ambient	102	(9)	a	165	(44)	a	190	(9)	a
elevated	112	(3)	a	203	(27)	a	206	(14)	a
		p = 0.16			p = 0.24			p = 0.96	

Table 2.5. Harvest data for *Spartina patens* in the mixed community. Mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1			Harvest 2			Harvest 3		
Julian day	150.0			230.5			292.7		
Shoot density (shoots m-2)									
control	1688	(465)	a	2820	(830)	a	3064	(801)	a
ambient	1852	(302)	a	2544	(579)	a	2544	(582)	a
elevated	1656	(440)	a	2032	(566)	a	1988	(593)	a
		p = 0.69			p = 0.34			p = 0.31	
Total biomass (g m-2)									
control	81.0	(25.7)	a	383.5	(133)	a	365.7	(114)	a
ambient	84.9	(18.6)	a	340.6	(79.8)	a	368.3	(116)	a
elevated	75.2	(26.0)	a	299.2	(79.4)	a	250.1	(75.1)	a
		p = 0.74			p = 0.53			p = 0.42	
Green biomass (g m-2)									
control	81.0	(25.7)	a	331.4	(115)	a	209.6	(63.5)	a
ambient	84.9	(18.6)	a	302.7	(70.5)	a	267.3	(90.6)	a
elevated	75.2	(26.0)	a	268.9	(70.9)	a	178.6	(49.6)	a
		p = 0.74			p = 0.61			p = 0.44	
Mean shoot weight (mg)									
control	46.2	(5.7)	a	128	(18)	a	117	(17)	a
ambient	44.0	(3.1)	a	133	(16)	a	136	(13)	a
elevated	43.3	(8.3)	a	151	(12)	a	126	(3)	a
		p = 0.77			p = 0.61			p = 0.51	
Stem / leaf ratio (dry weight)									
control	1.74	(0.08)	a	1.14	(0.1)	a	3.21	(0.04)	a
ambient	1.79	(0.14)	a	1.08	(0.11)	a	1.79	(0.13)	b
elevated	1.95	(0.17)	a	1.14	(0.05)	a	1.20	(0.42)	b
		p = 0.35			p = 0.78			p = 0.002	
reproduction (% flowering)									
control	0	(0)	a	3.9	(2.2)	a	2.0	(1.3)	a
ambient	0	(0)	a	1.6	(0.5)	a	2.3	(1.7)	a
elevated	0	(0)	a	0.3	(0.3)	a	4.9	(4.9)	a
					p = 0.15			p = 0.69	
% Senescence (% dry weight)									
control	0	(0)	a	12.7	(1.7)	a	41.1	(4.8)	b
ambient	0	(0)	a	11.3	(1.9)	ab	27.4	(3.0)	a
elevated	0	(0)	a	10.0	(0.8)	b	26.7	(4.7)	a
					p = 0.10			p = 0.02	
Specific leaf weight (g m-2)									
control	124.0	(12.5)	a	190.5	(7.5)	a	177.8	(6.5)	a
ambient	113.2	(8.0)	a	194.2	(8.1)	a	193.6	(1.9)	a
elevated	108.9	(13.3)	a	197.3	(10.1)	a	296.0	(60.8)	b
		p = 0.28			p = 0.51			p = 0.06	

Table 2.6. Harvest data for *Distichlis spicata* in the mixed community. Mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1			Harvest 2			Harvest 3		
Julian day	150.0			230.5			292.7		
Shoot density (shoots m-2)									
control	1632	(941)	a	1428	(678)	a	1300	(643)	a
ambient	1084	(113)	a	1096	(233)	a	836	(185)	a
elevated	1260	(437)	a	1600	(444)	a	1224	(425)	a
		p = 0.73			p = 0.54			p = 0.63	
Total biomass (g m-2)									
control	102.9	(56.8)	a	240.3	(102)	a	198.8	(101)	a
ambient	100.7	(12.6)	a	179.7	(42.2)	a	150.5	(24.5)	a
elevated	110.1	(29.0)	a	268.7	(88.0)	a	230.0	(96.4)	a
		p = 0.97			p = 0.55			p = 0.68	
Green biomass (g m-2)									
control	102.9	(56.8)	a	212.0	(87.5)	a	138.4	(73.1)	a
ambient	100.7	(12.6)	a	164.0	(39.5)	a	106.7	(17.6)	a
elevated	110.1	(29.0)	a	242.9	(76.8)	a	156.7	(60.4)	a
		p = 0.97			p = 0.58			p = 0.74	
Mean shoot weight (mg)									
control	77.9	(14.3)	a	178	(33)	a	145	(23)	a
ambient	94.3	(10.5)	a	166	(16)	a	202	(33)	a
elevated	80.6	(16.3)	a	153	(18)	a	182	(16)	a
		p = 0.52			p = 0.74			p = 0.34	
Stem / leaf ratio (dry weight)									
control	2.07	(0.13)	a	2.03	(0.21)	a	11.31	(2.49)	a
ambient	2.05	(0.19)	a	2.40	(0.19)	a	3.98	(0.44)	b
elevated	3.01	(0.76)	a	2.33	(0.19)	a	4.62	(2.18)	ab
		p = 0.26			p = 0.24			p = 0.088	
reproduction (flowers m-2)									
control	0	(0)	a	7.3	(3.7)	a	16.5	(4.6)	a
ambient	0	(0)	a	15.7	(4.8)	b	40.1	(13.4)	ab
elevated	0	(0)	a	13.2	(5.6)	ab	30.7	(10.3)	b
					p = 0.092			p = 0.097	
% Senescence (% dry weight)									
control	0	(0)	a	10.9	(1.6)	a	35.8	(4.3)	a
ambient	0	(0)	a	8.9	(1.8)	a	29.2	(2.1)	a
elevated	0	(0)	a	8.3	(1.5)	a	28.6	(4.2)	a
					p = 0.37			p = 0.38	
Specific leaf weight (g m-2)									
control	115.8	(14.1)	a	170.0	(27.9)	a	132.8	(12.0)	a
ambient	107.5	(3.6)	a	137.6	(10.6)	a	128.0	(4.6)	a
elevated	98.6	(12.8)	a	151.2	(7.0)	a	172.3	(28.4)	a
		p = 0.59			p = 0.28			p = 0.16	

Table 2.7. Belowground biomass in regrowth cores, separated in four 5 cm segments. Mean and standard error of 11 cores. Means with the same letter are not significantly different at the 0.05 level.

Core segment	0 – 5 cm			5 – 10 cm			10 – 15 cm			15 -20 cm		
Scirpus olneyi in C3 community												
Roots												
control	36.7	(3.05)	a	37.24	(4.70)	a	40.75	(5.81)	a	38.94	(5.42)	a
ambient	50.05	(3.29)	a	40.06	(5.67)	a	47.61	(5.31)	a	43.95	(5.81)	a
elevated	82.25	(9.55)	b	67.53	(9.81)	b	79.05	(9.41)	b	67.82	(21.1)	a
		p = 0.0001			p = 0.0087			p = 0.013			p = 0.251	
Rhizomes												
control	3.81	(2.57)	a	23.68	(15.3)	a	99.82	(50.5)	a	6.36	(6.36)	a
ambient	38.35	(21.9)	a	123.5	(56.2)	a	42.01	(40.9)	a	6.20	(6.20)	a
elevated	38.21	(13.6)	a	103.1	(50.5)	a	19.03	(11.1)	a	23.11	(18.4)	a
		p = 0.19			p = 0.26			p = 0.31			p = 0.50	
Spartina in C4 community												
Roots												
control	139.5	(17.1)	a	34.22	(6.26)	a	5.95	(2.95)	a	2.19	(1.93)	a
ambient	85.23	(8.63)	b	27.70	(5.65)	a	6.14	(1.87)	a	0.88	(0.42)	a
elevated	108.4	(13.2)	ab	35.35	(7.57)	a	8.21	(3.93)	a	1.45	(0.96)	a
		p = 0.027			p = 0.68			p = 0.85			p = 0.77	
Rhizomes												
control	93.46	(13.7)	a	7.31	(3.74)	a	0.0	(0.0)	a	0.0	(0.0)	a
ambient	84.11	(15.2)	a	9.18	(5.38)	a	3.23	(3.23)	a	1.02	(1.02)	a
elevated	115.9	(22.2)	a	3.91	(2.09)	a	1.70	(1.70)	a	0.0	(0.0)	a
		p = 0.42			p = 0.64			p = 0.56			p = 0.40	
Mixed community												
Roots (C3 + C4)												
control	97.79	(12.0)	a	34.20	(8.39)	a	11.93	(4.64)	a	2.00	(1.49)	a
ambient	123.7	(15.4)	a	38.07	(6.50)	a	14.21	(4.10)	a	2.07	(1.00)	a
elevated	120.5	(11.1)	a	52.55	(7.33)	a	33.03	(6.47)	b	17.24	(4.99)	b
		p = 0.32			p = 0.20			p = 0.013			p = 0.0014	
Rhizomes (C3)												
control	7.36	(7.36)	a	15.25	(12.4)	a	4.73	(4.73)	a	0.0	(0.0)	a
ambient	0.0	(0.0)	a	0.39	(0.39)	a	1.84	(1.84)	a	0.0	(0.0)	a
elevated	38.26	(23.9)	a	12.62	(8.55)	a	7.63	(5.41)	a	2.24	(2.24)	a
		p = 0.159			p = 0.45			p = 0.64			p = 0.38	
Rhizomes (C4)												
control	78.78	(13.9)	a	0.0	(0.0)	a	2.29	(1.96)	a	0.0	(0.0)	a
ambient	101.3	(11.7)	a	19.45	(12.1)	a	0.0	(0.0)	a	0.0	(0.0)	a
elevated	90.05	(12.1)	a	29.58	(13.7)	a	1.47	(1.47)	a	0.0	(0.0)	a
		p = 0.46			p = 0.148			p = 0.52				

Table 2.8. Belowground biomass in original cores, separated in four 5 cm segments. The fraction with organic matter > 2mm consists of root, stem and leaf tissue. Mean and standard error of 4 cores. Means with the same letter are not significantly different at the 0.05 level.

Scirpus olneyi in C3 community

Core segment	0 - 5 cm			5 - 10 cm			10 - 15 cm			Total		
Rhizomes (g m-2)												
control	689.7	(369)	a	1435	(660)	a	223	(102)	a	2358	(538)	a
ambient	758.2	(365)	a	1329	(510)	a	207	(207)	a	2294	(252)	a
elevated	627.0	(186)	a	1094	(400)	a	935	(353)	a	2556	(364)	a
Fraction > 2 mm (g m-2)												
control	1652	(161)	a	452.9	(49.3)	a	738.2	(66.4)	a	565.2	(63.1)	a
ambient	1293	(446)	a	486.9	(40.8)	a	789.9	(120)	a	696.5	(141)	a
elevated	1864	(205)	a	466.2	(39.3)	a	812.2	(67.3)	a	794.5	(57.0)	a

Spartina patens in C4 community

Core segment	0 - 5 cm			5 - 10 cm			10 - 15 cm			15 - 20 cm		
Rhizomes (g m-2)												
control	535	(66)	a	10	(5)	a	0	(0)	a	0	(0)	a
ambient	499	(87)	a	15	(10)	a	0	(0)	a	0	(0)	a
elevated	664	(109)	a	193	(143)	a	127	(110)	a	107	(91)	a
Fraction > 2 mm (g m-2)												
control	3782	(504)	a	2519	(357)	a	3451	(41)	a	2937	(564)	a
ambient	3540	(260)	a	2706	(196)	a	2602	(236)	a	3207	(142)	a
elevated	3772	(368)	a	3623	(467)	a	3025	(365)	a	3474	(204)	a

Chapter 3. Nitrogen.

Aboveground

Methods

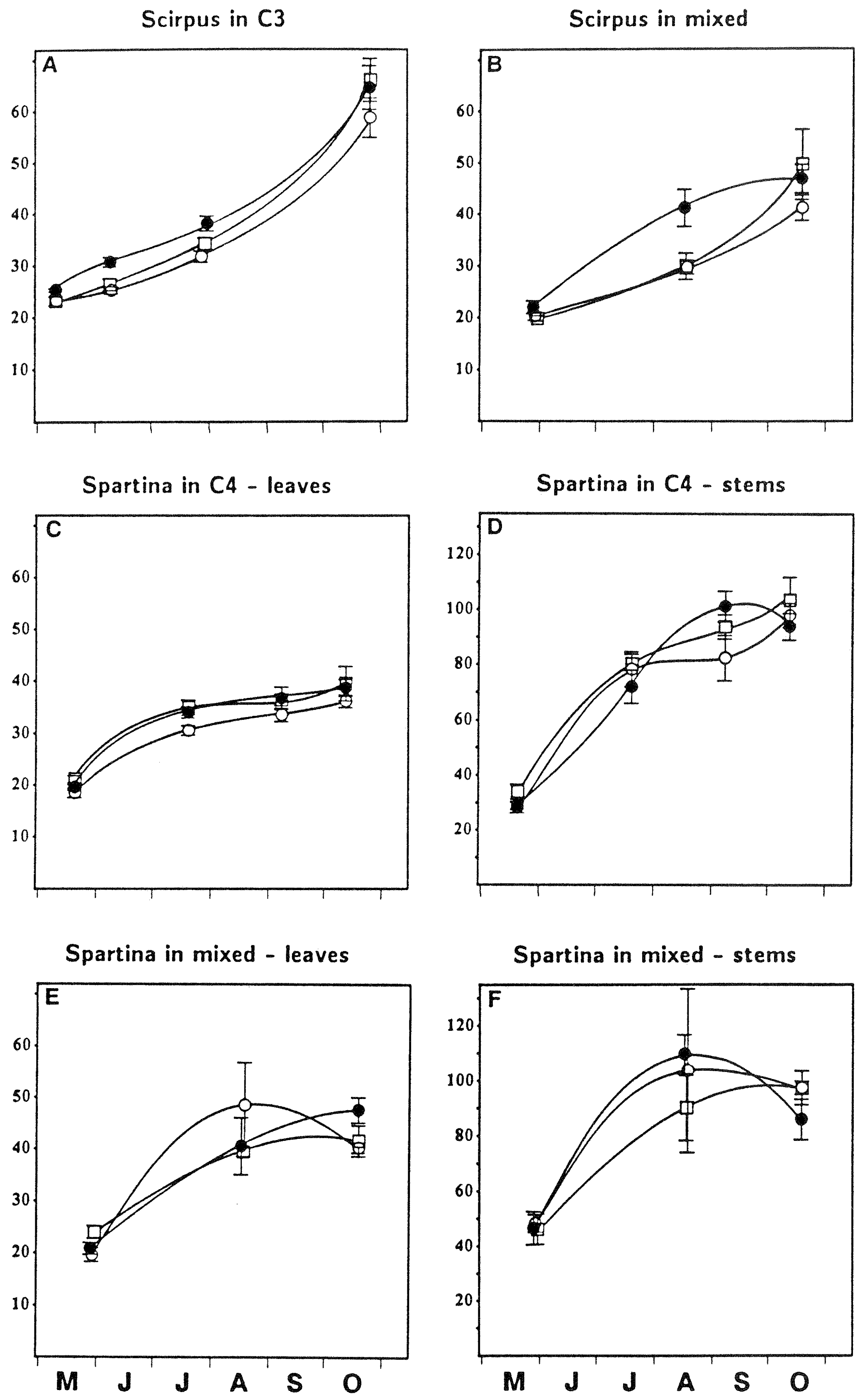
Aboveground plant material collected during the periodic sampling and belowground material from the regrowth cores was analyzed for carbon and nitrogen using a Carbon-Hydrogen-Nitrogen analyzer (Control Equipment Corp.) at the Horn Point Laboratory of the University of Maryland. The percent nitrogen and carbon on a weight basis, the C/N ratio and the total amount of nitrogen in the aboveground plant canopy per square meter surface area were calculated.

Results

Elevated CO_2 reduced the percent nitrogen and increased the carbon/nitrogen ratio in *Scirpus* stems, both in the pure and the mixed community (figure 3.1,table 3.1 and 3.2), but the difference is not significant at all harvests. Due to the slightly higher biomass in the elevated chambers of the pure *Scirpus* community no effect was found on the total amount of nitrogen per meter square (figure 3.2.A, table 3.3). In the mixed community the large expansion in *Scirpus* biomass resulted in a significant increase in the amount of nitrogen present in *Scirpus* fraction of the elevated chambers (figure 3.2.B, table 3.3).

Elevated CO_2 significantly reduced the percent nitrogen of *Scirpus* flower bracts, and there was a non-significant increase in the C/N ratio (table 3.4). There was no effect of elevated CO_2 on the nitrogen content of the seeds.

No consistent correlation between tissue nitrogen concentration and physical location within the *Scirpus* community was found. There was a block effect on total nitrogen was within the *Scirpus* community, correlated with the large block effect on total biomass (figure 2.4, table 2.6).


Scirpus in C3

Scirpus in mixed

Spartina in C4 - leaves

Spartina in C4 - stems

Spartina in mixed - leaves

Spartina in mixed - stems

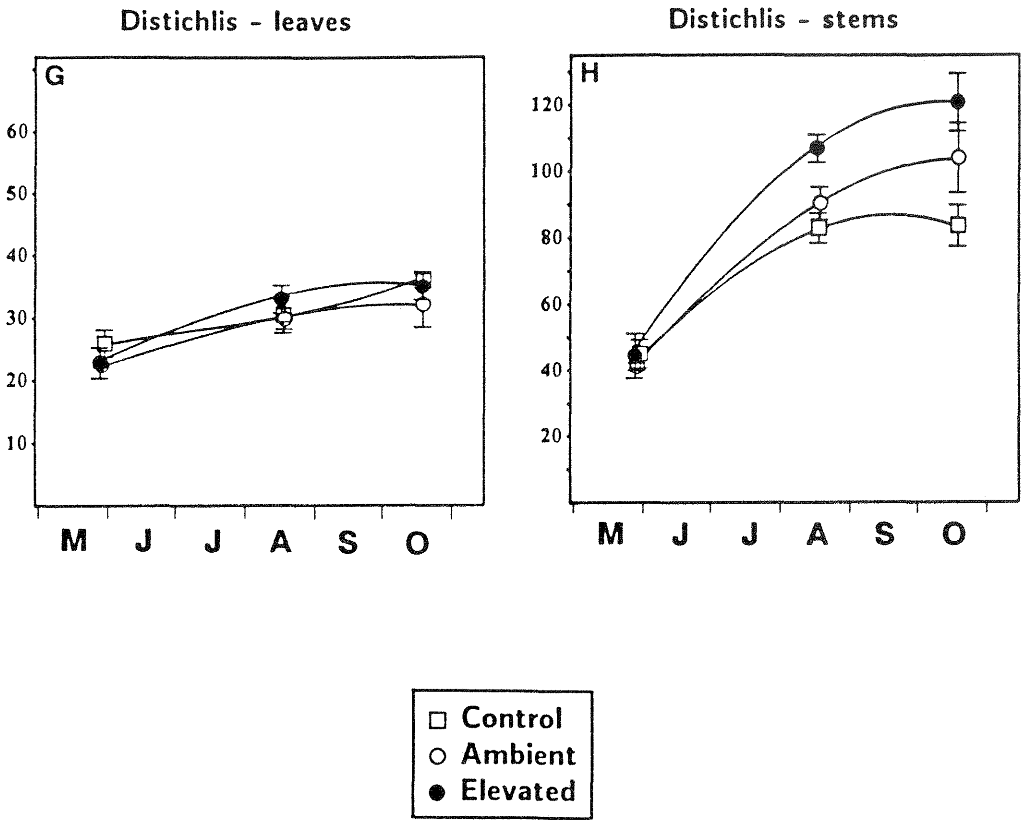
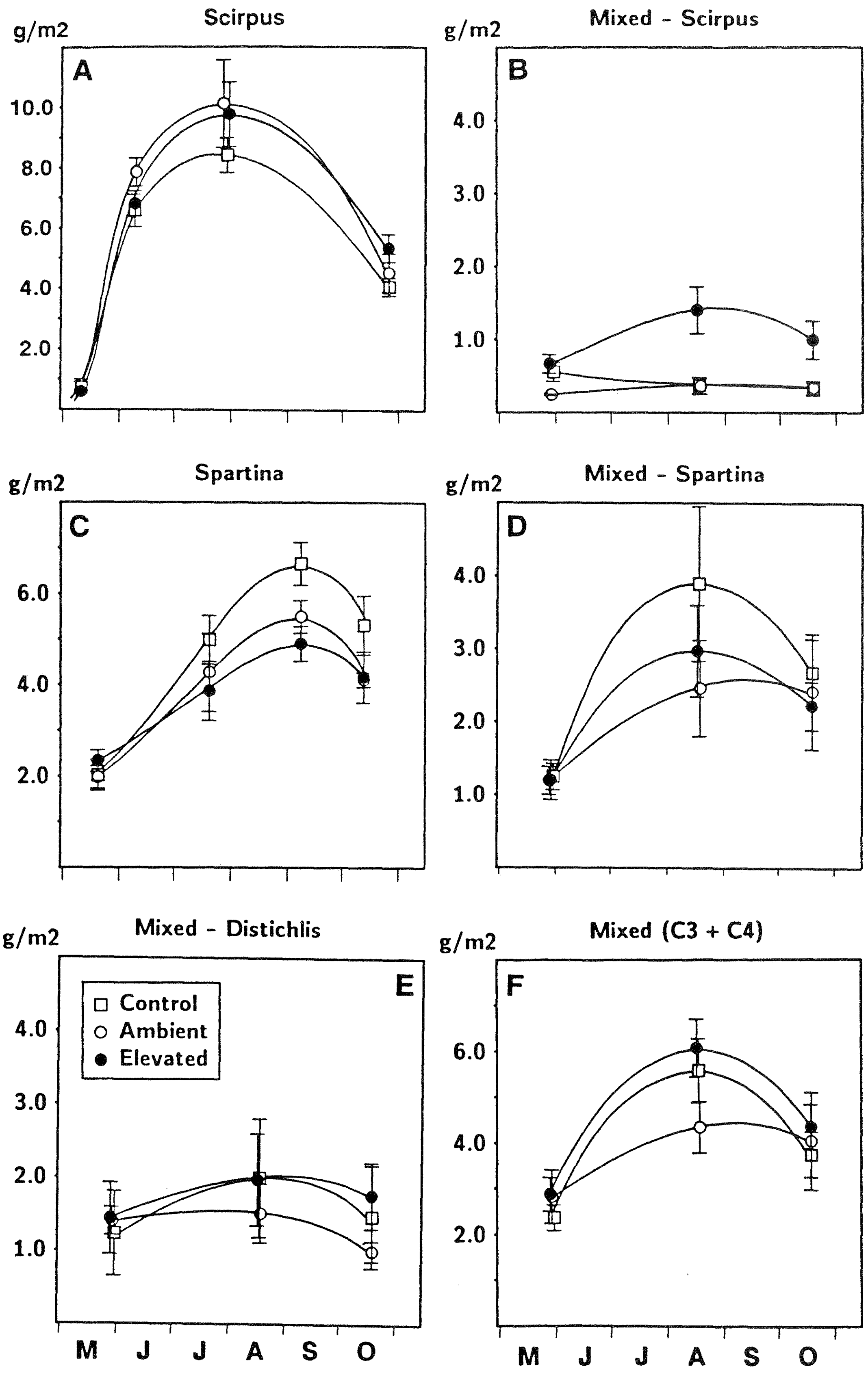


Figure 3.1. Carbon / nitrogen ratio of aboveground plant tissue collected during the harvests of 1988. A. *Scirpus* in C_3 community, B. *Scirpus* in mixed community, C. *Spartina* in C_4 community : leaves, D. *Spartina* in C_4 community : stems, E. *Spartina* in mixed community : leaves, F. *Spartina* in mixed community : stems, G. *Distichlis* leaves, H. *Distichlis* stems. Values are mean and standard error for five chambers.


Scirpus
g/m2
A
10.0
8.0
6.0
4.0
2.0
Mixed - Scirpus
g/m2
B
4.0
3.0
2.0
1.0
Spartina
g/m2
C
6.0
4.0
2.0
Mixed - Spartina
g/m2
D
4.0
3.0
2.0
1.0
Mixed - Distichlis
g/m2
E
□ Control
○ Ambient
● Elevated
4.0
3.0
2.0
1.0
M J J A S O
Mixed (C3 + C4)
g/m2
F
6.0
4.0
2.0
M J J A S O

There was no effect of elevated CO_2 on C/N ratio or percent nitrogen for *Spartina*, either in the pure or mixed community (tables 3.1, 3.2). The total amount of nitrogen per meter square therefore reflects the total biomass per meter ground area. A large difference was found between the nitrogen content of leaf and stem tissue, the leaves having a two to three times higher nitrogen concentration than the stems.

Elevated CO_2 decreased the nitrogen content (increased the C/N ratio) of *Distichlis* stems (figure 3.1.H), but no effect was found on the nitrogen content of the leaves, or on the total amount of nitrogen per meter square (figure 3.2).

The total amount of nitrogen present in the aboveground vegetation was higher in the *Scirpus* community than in the *Spartina* or mixed community (figure 3.2). This could be caused by a deeper penetrating root system providing access to additional nitrogen sources. The increase in *Scirpus* biomass in the elevated chambers of the mixed community resulted in an overall increase in the total amount of nitrogen in the aboveground vegetation.

←

Figure 3.2. Total amount of nitrogen in aboveground tissues per m^2. A. *Scirpus* in C_3 community, B. *Scirpus* in mixed community, C. *Spartina* in C_4 community, D. *Spartina* in mixed community, E. *Distichlis*, F. Total nitrogen in mixed community. Values are mean and standard error of five chambers.

Belowground

In all communities the mean nitrogen content of roots and rhizomes was lower in the regrowth cores from elevated chambers than in cores from ambient chambers (figure 3.3, table 3.5), but this effect is significant only for *Spartina* rhizomes. The trend in reduced nitrogen content in belowground tissues is observed in all three communities but the small sample size and large variability obscure the statistical significance. The number of samples of *Scirpus* rhizome in the mixed community was too small to use in the analysis.

It is not possible to tell how much nitrogen is stored in belowground tissue because the regrowth cores do not give a accurate estimate of the total biomass belowground, and the nitrogen concentration of the young roots and rhizomes in the regrowth cores may not reflect the nitrogen concentration in older roots and rhizomes. The cores also do not show how much biomass and nitrogen is present more than 20 cm below the soil surface .

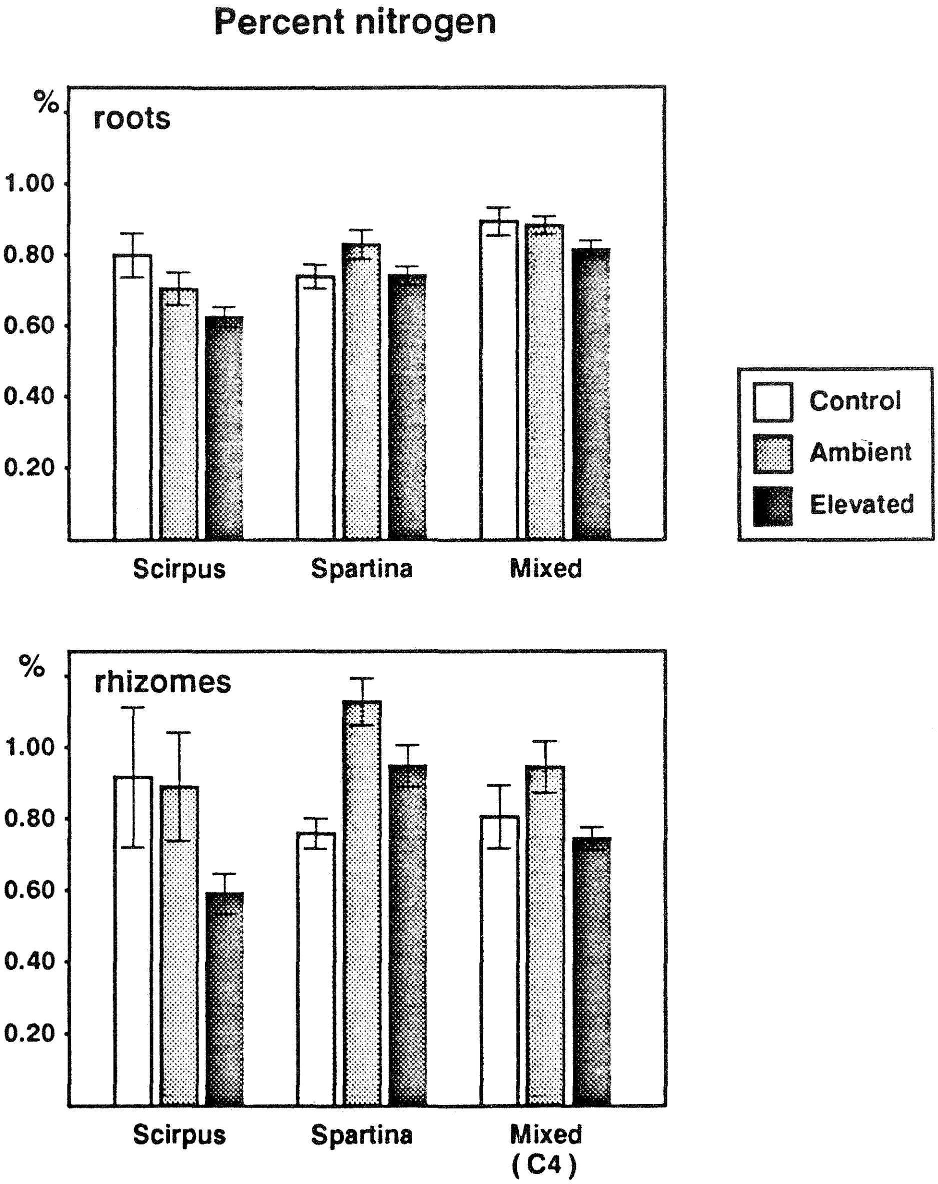


Figure 3.3. Percent nitrogen in belowground tissue in regrowth cores of the *Scirpus*, *Spartina* and mixed community. A. Roots, B. Rhizomes. Values are mean and standard error.

Table 3.1. Percent nitrogen in aboveground tissues. Values are mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1	Harvest 2	Harvest 3	Harvest 4
Scirpus olneyi in C3 community				
Green stems				
control	1.93 (0.07) a	1.70 (0.07) a	1.32 (0.04) a	0.68 (0.04) a
ambient	1.91 (0.07) a	1.74 (0.04) a	1.40 (0.04) a	0.76 (0.05) a
elevated	1.75 (0.02) a	1.44 (0.04) b	1.18 (0.04) a	0.69 (0.04) a
	p = 0.15	p = 0.008	p = 0.32	p = 0.29
Senescent stems				
control	. (.)	. (.)	1.40 (0.16) a	0.94 (0.06) a
ambient	. (.)	. (.)	1.28 (0.10) a	0.73 (0.05) b
elevated	. (.)	. (.)	1.43 (0.09) a	0.63 (0.02) c
			p = 0.54	p = 0.0001
Spartina in C4 community				
Green stems				
control	1.37 (0.10) a	0.59 (0.03) a	0.50 (0.03) a	0.46 (0.04) a
ambient	1.63 (0.13) a	0.61 (0.05) a	0.59 (0.06) a	0.47 (0.02) a
elevated	1.56 (0.07) a	0.67 (0.06) a	0.47 (0.03) a	0.50 (0.02) a
	p = 0.26	p = 0.43	p = 0.09	p = 0.57
Green leaves				
control	2.11 (0.07) a	1.30 (0.06) a	1.23 (0.04) a	1.15 (0.10) a
ambient	2.37 (0.07) a	1.45 (0.04) b	1.32 (0.05) a	1.20 (0.04) a
elevated	2.25 (0.12) a	1.33 (0.05) ab	1.22 (0.07) a	1.14 (0.05) a
	p = 0.12	p = 0.10	p = 0.44	p = 0.79
Senescent shoots				
control	. (.)	0.58 (0.05) a	0.59 (0.06) a	0.54 (0.02) a
ambient	. (.)	0.59 (0.02) a	0.67 (0.04) a	0.65 (0.05) b
elevated	. (.)	0.63 (0.07) a	0.62 (0.07) a	0.58 (0.04) ab
		p = 0.67	p = 0.44	p = 0.12

	Harvest 1		Harvest 2		Harvest 3	
Scirpus olneyi in Mixed community						
Green stems						
control	2.23	(0.06) a	1.49	(0.10) a	0.96	(0.15) a
ambient	2.16	(0.08) a	1.33	(0.09) ab	1.05	(0.06) a
elevated	2.01	(0.11) a	1.10	(0.11) b	0.95	(0.05) a
		p = 0.18		p = 0.08		p = 0.77
Senescent stems						
control	.	(.)	.	(.)	1.04	(0.06) a
ambient	.	(.)	.	(.)	1.01	(0.08) a
elevated	.	(.)	.	(.)	0.81	(0.09) a
						p = 0.10
Spartina in Mixed community						
Green stems						
control	1.05	(0.12) a	0.56	(0.09) a	0.48	(0.01) a
ambient	0.97	(0.07) a	0.60	(0.16) a	0.49	(0.03) a
elevated	1.07	(0.15) a	0.43	(0.03) a	0.56	(0.06) a
		p = 0.77		p = 0.45		p = 0.45
Green leaves						
control	1.94	(0.11) a	1.14	(0.02) a	1.11	(0.09) a
ambient	2.38	(0.17) b	0.88	(0.10) a	1.10	(0.02) a
elevated	2.22	(0.12) ab	1.18	(0.20) a	0.95	(0.05) a
		p = 0.08		p = 0.25		p = 0.25
Senescent stems						
control	.	(.)	0.66	(0.04) a	0.56	(0.01) a
ambient	.	(.)	0.52	(0.06) a	0.54	(0.05) a
elevated	.	(.)	0.59	(0.04) a	0.63	(0.09) a
				p = 0.35		p = 0.47
Distichlis in Mixed community						
Green stems						
control	1.04	(0.12) a	0.58	(0.04) a	0.58	(0.04) a
ambient	1.09	(0.04) a	0.53	(0.03) ab	0.47	(0.05) ab
elevated	1.11	(0.21) a	0.45	(0.02) b	0.40	(0.03) b
		p = 0.86		p = 0.02		p = 0.07
Green leaves						
control	1.77	(0.19) a	1.54	(0.15) a	1.31	(0.11) a
ambient	1.96	(0.04) a	1.53	(0.10) a	1.42	(0.06) a
elevated	2.03	(0.25) a	1.40	(0.11) a	1.32	(0.08) a
		p = 0.41		p = 0.66		p = 0.58
Senescent shoots						
control	.	(.)	0.77	(0.07) a	0.90	(0.22) a
ambient	.	(.)	0.65	(0.05) ab	0.69	(0.06) a
elevated	.	(.)	0.57	(0.02) b	0.56	(0.03) a
				p = 0.11		p = 0.36

Table 3.2. Carbon / nitrogen ratio of aboveground tissues. Values are mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1		Harvest 2		Harvest 3		Harvest 4	
Scirpus olneyi in C3 community								
Green stems								
control	23.18	(0.85) a	26.31	(1.14) a	34.29	(1.18) a	66.10	(4.17) a
ambient	23.25	(0.89) a	25.25	(0.66) a	31.73	(1.10) a	58.79	(3.82) a
elevated	25.30	(0.27) a	30.67	(0.94) b	38.17	(1.48) a	64.60	(4.22) a
		p = 0.16		p = 0.0004		p = 0.24		p = 0.39
Senescent stems								
control	.	(.)	.	(.)	34.62	(4.46) a	47.64	(3.12) a
ambient	.	(.)	.	(.)	35.05	(2.73) a	54.19	(6.03) a
elevated	.	(.)	.	(.)	32.59	(2.20) a	67.03	(2.46) b
						p = 0.74		p = 0.002
Spartina in C4 community								
Green stems								
control	33.95	(2.78) a	80.10	(3.55) a	93.73	(4.48) ab	103.5	(8.52) a
ambient	28.17	(2.03) a	78.17	(6.25) a	82.43	(8.18) a	98.07	(4.45) a
elevated	28.93	(1.37) a	71.91	(5.84) a	101.2	(5.65) b	93.81	(4.85) a
		p = 0.19		p = 0.58		p = 0.07		p = 0.44
Green leaves								
control	21.11	(0.69) a	34.88	(1.43) a	36.33	(1.06) a	39.48	(3.33) a
ambient	18.53	(0.93) b	30.55	(0.91) b	33.53	(1.29) a	36.10	(1.20) a
elevated	19.58	(0.57) ab	33.97	(1.08) ab	36.67	(2.16) a	38.61	(1.62) a
		p = 0.05		p = 0.06		p = 0.34		p = 0.46
Senescent stems								
control	.	(.)	84.61	(8.22) a	82.13	(6.37) a	83.57	(3.51) a
ambient	.	(.)	74.49	(2.93) a	69.76	(4.82) a	67.77	(4.96) b
elevated	.	(.)	73.32	(8.87) a	77.72	(8.16) a	77.42	(5.18) ab
				p = 0.44		p = 0.27		p = 0.11

	Harvest 1			Harvest 2			Harvest 3		
<u>Scirpus olneyi in Mixed community</u>									
Green stems									
control	19.79	(0.54)	a	29.81	(2.56)	a	49.44	(6.81)	a
ambient	20.32	(0.83)	a	29.60	(1.32)	a	40.98	(2.47)	a
elevated	22.04	(1.22)	a	41.1	(3.60)	b	46.72	(2.76)	a
		p = 0.18			p = 0.03			p = 0.51	
Senescent stems									
control	.	(.)		.	(.)		41.20	(2.51)	ab
ambient	.	(.)		.	(.)		33.70	(2.39)	a
elevated	.	(.)		.	(.)		50.20	(4.23)	b
								p = 0.02	
<u>Spartina in Mixed community</u>									
Green stems									
control	46.22	(5.49)	a	89.91	(11.8)	a	97.28	(2.48)	a
ambient	48.39	(3.13)	a	103.6	(29.7)	a	97.26	(6.21)	a
elevated	46.54	(5.99)	a	109.5	(7.04)	a	85.82	(7.29)	a
		p = 0.93			p = 0.75			p = 0.45	
Green leaves									
control	24.02	(1.25)	a	39.52	(0.89)	a	41.62	(2.98)	a
ambient	19.61	(1.34)	b	48.50	(8.26)	a	40.33	(1.01)	a
elevated	20.90	(1.14)	ab	40.54	(5.50)	a	47.60	(2.47)	a
		p = 0.07			p = 0.63			p = 0.17	
Senescent stems									
control	.	(.)		69.77	(4.84)	a	80.65	(2.08)	a
ambient	.	(.)		92.47	(13.9)	a	84.10	(7.15)	a
elevated	.	(.)		75.54	(7.83)	a	76.46	(14.6)	a
					p = 0.44			p = 0.78	
<u>Distichlis in Mixed community</u>									
Green stems									
control	44.97	(4.25)	a	82.70	(4.45)	a	83.58	(6.20)	a
ambient	41.12	(1.18)	a	90.09	(4.85)	a	103.9	(10.5)	ab
elevated	44.40	(6.75)	a	106.6	(4.19)	b	120.7	(8.78)	b
		p = 0.65			p = 0.01			p = 0.08	
Green leaves									
control	25.91	(2.20)	a	30.51	(2.93)	a	36.09	(1.35)	a
ambient	22.49	(0.33)	a	29.80	(1.59)	a	32.21	(3.63)	a
elevated	22.87	(2.44)	a	32.96	(2.22)	a	35.08	(2.03)	a
		p = 0.27			p = 0.63			p = 0.52	
Senescent stems									
control	.	(.)		60.50	(6.10)	a	59.39	(9.99)	a
ambient	.	(.)		68.24	(4.68)	ab	66.92	(5.02)	a
elevated	.	(.)		77.58	(3.08)	b	80.38	(2.82)	a
					p = 0.11			p = 0.22	

Table 3.3. Total aboveground nitrogen in g m^{-2}. Mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	Harvest 1		Harvest 2		Harvest 3		Harvest 4	
Scirpus olneyi in C3 community								
Green biomass								
control	0.71	(0.20) a	6.43	(0.54) a	7.63	(0.80) a	1.36	(0.34) a
ambient	0.80	(0.20) a	7.62	(0.48) a	9.42	(1.62) a	2.74	(0.67) a
elevated	0.58	(0.05) a	6.68	(0.42) a	9.32	(1.10) a	3.41	(0.55) a
		p = 0.96		p = 0.96		p = 0.95		p = 0.54
Total biomass								
control	0.71	(0.20) a	6.56	(0.54) a	7.88	(0.98) a	4.05	(0.30) a
ambient	0.80	(0.20) a	7.83	(0.47) a	10.1	(1.45) a	4.52	(0.64) a
elevated	0.58	(0.05) a	6.79	(0.42) a	9.75	(1.07) a	5.34	(0.46) a
		p = 0.96		p = 0.96		p = 0.92		p = 0.91
Spartina in C4 community								
Green leaves								
control	0.98	(0.13) a	3.00	(0.33) a	4.03	(0.33) a	2.39	(0.27) a
ambient	0.89	(0.09) a	2.78	(0.58) a	3.52	(0.23) a	2.24	(0.11) a
elevated	1.14	(0.12) a	2.35	(0.44) a	3.22	(0.25) a	2.05	(0.38) a
		p = 0.32		p = 0.58		p = 0.18		p = 0.75
Green stems								
control	1.03	(0.20) a	1.53	(0.21) a	2.05	(0.15) a	1.72	(0.27) a
ambient	1.09	(0.17) a	1.20	(0.24) a	1.65	(0.19) a	1.20	(0.07) a
elevated	1.42	(0.14) a	1.27	(0.22) a	1.28	(0.15) a	1.27	(0.23) a
		p = 0.29		p = 0.56		p = 0.05		p = 0.27
Total biomass								
control	2.01	(0.33) a	4.98	(0.54) a	6.65	(0.47) a	5.31	(0.65) a
ambient	1.97	(0.25) a	4.27	(0.86) a	5.49	(0.36) ab	4.11	(0.16) a
elevated	2.56	(0.24) a	3.86	(0.65) a	4.90	(0.38) b	4.17	(0.56) a
		p = 0.29		p = 0.57		p = 0.042		p = 0.23

	Harvest 1			Harvest 2			Harvest 3		
Scirpus olneyi in Mixed community									
Green stems									
control	0.55	(0.13)	a	0.37	(0.11)	a	0.13	(0.04)	a
ambient	0.24	(0.01)	a	0.36	(0.11)	a	0.16	(0.04)	a
elevated	0.66	(0.13)	a	1.40	(0.32)	b	0.68	(0.18)	b
		p = 0.059			p = 0.0053			p = 0.0143	
Total Scirpus									
control	0.55	(0.13)	a	0.37	(0.11)	a	0.32	(0.09)	a
ambient	0.24	(0.01)	a	0.36	(0.11)	a	0.34	(0.09)	a
elevated	0.66	(0.13)	a	1.40	(0.32)	b	0.99	(0.26)	b
		p = 0.059			p = 0.0053			p = 0.0421	
Spartina in Mixed community									
Green leaves									
control	0.62	(0.10)	a	2.19	(0.54)	a	0.67	(0.09)	a
ambient	0.62	(0.17)	a	1.29	(0.33)	a	1.10	(0.41)	a
elevated	0.60	(0.11)	a	1.96	(0.55)	a	1.15	(0.35)	a
		p = 0.99			p = 0.39			p = 0.57	
Green stems									
control	0.62	(0.08)	a	1.29	(0.44)	a	0.95	(0.15)	a
ambient	0.57	(0.11)	a	0.96	(0.41)	a	0.79	(0.23)	a
elevated	0.59	(0.09)	a	0.77	(0.08)	a	0.59	(0.13)	a
		p = 0.93			p = 0.63			p = 0.46	
Total Spartina									
control	1.24	(0.18)	a	3.89	(1.06)	a	2.68	(0.46)	a
ambient	1.20	(0.27)	a	2.46	(0.66)	a	2.42	(0.79)	a
elevated	1.19	(0.19)	a	2.97	(0.63)	a	2.22	(0.33)	a
		p = 0.98			p = 0.46			p = 0.88	
Distichlis in Mixed community									
Green leaves									
control	0.60	(0.30)	a	1.05	(0.43)	a	0.20	(0.10)	a
ambient	0.79	(0.12)	a	0.81	(0.25)	a	0.30	(0.04)	a
elevated	0.74	(0.28)	a	1.09	(0.36)	a	0.62	(0.23)	a
		p = 0.88			p = 0.83			p = 0.11	
Green stems									
control	0.63	(0.27)	a	0.76	(0.31)	a	0.74	(0.41)	a
ambient	0.64	(0.06)	a	0.59	(0.14)	a	0.40	(0.08)	a
elevated	0.69	(0.22)	a	0.73	(0.23)	a	0.63	(0.28)	a
		p = 0.97			p = 0.87			p = 0.70	
Total Distichlis									
control	1.23	(0.58)	a	1.99	(0.81)	a	1.47	(0.70)	a
ambient	1.40	(0.19)	a	1.51	(0.40)	a	1.00	(0.14)	a
elevated	1.44	(0.49)	a	1.97	(0.63)	a	1.76	(0.45)	a
		p = 0.94			p = 0.84			p = 0.57	

Table 3.4. Percent nitrogen and carbon/nitrogen ratio of flower bracts and seeds of *Scirpus olneyi* in the C_3 community. Values are mean and standard error of five chambers. Means with the same letter are not significantly different at the 0.05 level.

	% Nitrogen	C / N ratio
Scirpus olneyi in C3 community		
Flower bracts		
control	1.498 (.013) a	32.10 (0.30) a
ambient	1.178 (.093) b	42.93 (5.37) ab
elevated	0.980 (.087) b	49.64 (5.34) b
	p = 0.006	p = 0.08
Seeds		
control	0.934 (.096) a	56.01 (5.98) a
ambient	1.048 (.133) a	48.11 (5.87) a
elevated	0.964 (.099) a	52.47 (5.89) a
	p = 0.77	p = 0.62

Table 3.5. Percent nitrogen in roots and rhizomes of regrowth cores. Means with the same letter are not significantly different at the 0.05 level.

	Rhizomes	Roots
Scirpus (C3)		
control	0.916 (.196) a	0.799 (.062) a
ambient	0.890 (.153) a	0.705 (.046) ab
elevated	0.593 (.055) a	0.626 (.029) b
	p = 0.178	p = 0.065
Spartina (C4)		
control	0.758 (.043) a	0.741 (.033) a
ambient	1.130 (.066) b	0.832 (.040) a
elevated	0.948 (.059) c	0.744 (.025) a
	p = 0.0008	p = 0.134
Mixed (C3+C4) (C4 rhizomes)		
control	0.805 (.089) a	0.895 (.039) a
ambient	0.946 (.073) ab	0.885 (.024) a
elevated	0.744 (.032) b	0.818 (.024) a
	p = 0.091	p = 0.132

Chapter 4. Single leaf photosynthesis.

Methods.

Measurements of single leaf photosynthesis were made for monocultures of the sedge *Scirpus olneyi* (C_3) and *Spartina patens* (C_4), grown at ambient or elevated CO_2 over two growing seasons in the field. A portable ADC gas analyzer and parkinson leaf chamber with attached mass flow unit were used on attached leaves in the field. Elevated test concentrations of CO_2 were obtained from cylinders of 680 ppm CO_2 in air. Both ambient and elevated airstreams were humidified by passing air through a water bath with a fixed temperature (at least 15 °C below ambient) to maintain VPD's of < 2.00 kPa within the Parkinson leaf chamber. Average temperature within the leaf chamber during measurements ranged from 25 to 38 °C during the course of the 1988 growing season. However, by October, minimum night-time temperatures had approached the freezing point. Light response curves for single leaves were generated by placing neutral density filters over the "window" of the leaf chamber. CO_2 uptake rates were then recorded after acclimation to the new light regime had occurred (typically 3-4 minutes). All photosynthetic measurements were made on fully expanded leaves.

Results.

The response of single-leaf photosynthesis to light is shown in figure 4.1 for *Scirpus olneyi* and in figure 4.2 for *Spartina patens*. Measurements were made on leaves grown in ambient CO_2 and on leaves grown in elevated CO_2. Two light response curves were produced for each leaf; one at ambient CO_2 (open circles), and one at elevated CO_2 (closed circles). Square symbols are means of maximum photosynthesis. The data shown in figures 4.1 and 4.2 were taken during July of 1987 and June/July of 1988. Exposure of both plant species to elevated CO_2 began in early May of 1987.

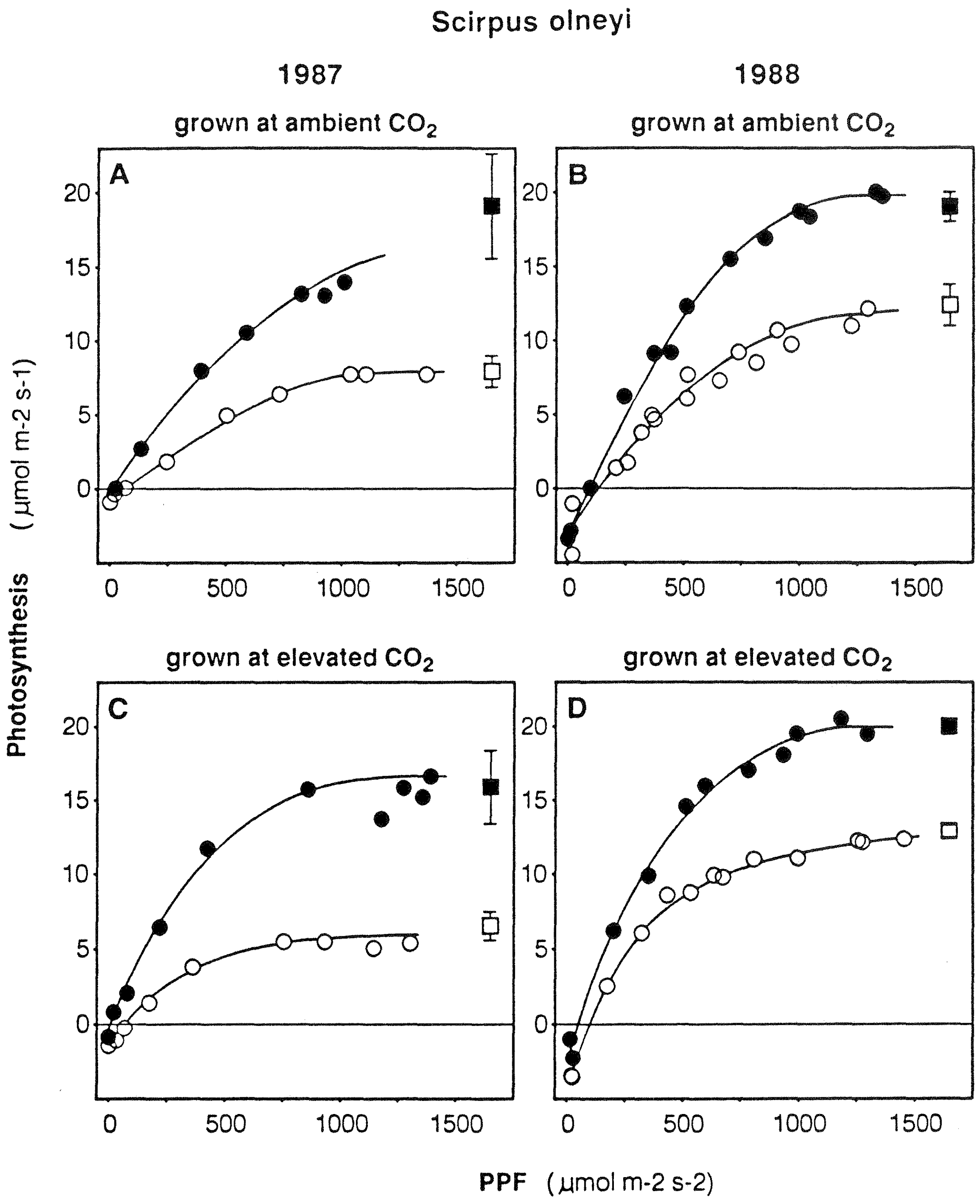


Figure 4.1. A comparison of light response curves for *Scirpus olneyi* plants grown at ambient and at elevated CO_2 for the years 1987 (July) and 1988 (June and July). A representative light response curve is shown for a leaf measured at ambient CO_2 (open circles) and at elevated CO_2 (closed circles). A square represents the mean maximum photosynthesis and standard error for all leaves measured at ambient (open square) and elevated CO_2 (closed square).

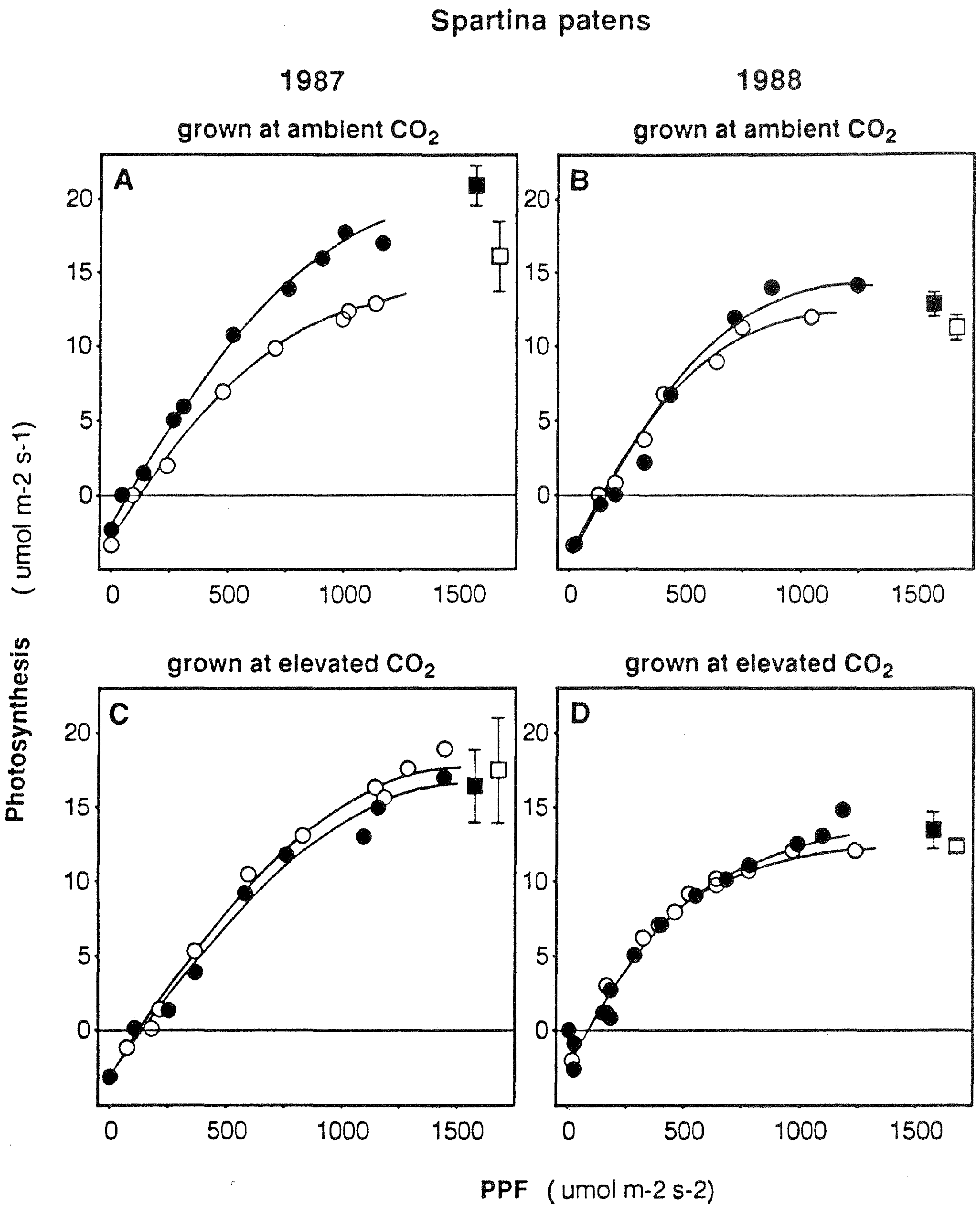


Figure 4.2. A comparison of light response curves for *Spartina patens* plants grown at ambient and at elevated CO_2 for the years 1987 (July) and 1988 (June and July). A representative light response curve is shown for a leaf measured at ambient CO_2 (open circles) and at elevated CO_2 (closed circles). A square represents the mean maximum photosynthesis and standard error for all leaves measured at ambient (open square) and elevated CO_2 (closed square).

Early summer data for both years of the experiment indicated clear differences in photosynthetic response to light between *Scirpus* and *Spartina*. In the *Scirpus*, photosynthesis at 680 ppm CO_2 was higher at all light levels above the compensation point when compared to plants grown or measured at ambient CO_2. No photosynthetic adjustment to high CO_2 was observed when results were compared between 1987 and 1988. Thus, plants grown at elevated CO_2 continued to respond to increased CO_2. In contrast, a smaller effect of elevated CO_2 on photosynthesis was observed in leaves of *Spartina* for either year of the experiment. The effect on *Spartina* was greatest in the spring and fall and least in midsummer.

In 1988, single leaf light response curves were also obtained throughout the growing season for *Scirpus* and *Spartina* (3-6 curves per species per day). Maximum photosynthesis for both species, grown and tested at ambient or elevated CO_2, is shown in figure 4.3. Significant differences in the maximum rate of photosynthesis between ambient and elevated CO_2 for *Scirpus olneyi* occurred between May and September. Lack of response to elevated CO_2 of *Scirpus* in October may be associated with the onset of lower temperatures and what has been termed O_2 (and as a consequence, CO_2) insensitive photosynthesis. Lack of response to CO_2 therefore may be associated with physiologically relevant temperatures as has been suggested by Sage and Sharkey (1987). Significant differences in maximum photosynthesis were observed only in late May/early June for *Spartina patens*. The initial response of photosynthesis to light was analyzed for each data set taken throughout the season using light as the independent variable. Analysis of this portion of the light response curves was used to determine the light compensation point and the initial slope of the light response curve. No consistent differences in either light response parameter was observed in *Spartina patens* (figure 4.4). However, *Scirpus olneyi* (figure 4.5), at elevated CO_2 showed a decline in light compensation point and an increase in the initial slope of the light response curve until late in the growing season (October). This is consistent with the maximum photosynthesis data obtained for this same species at 680 ppm CO_2.

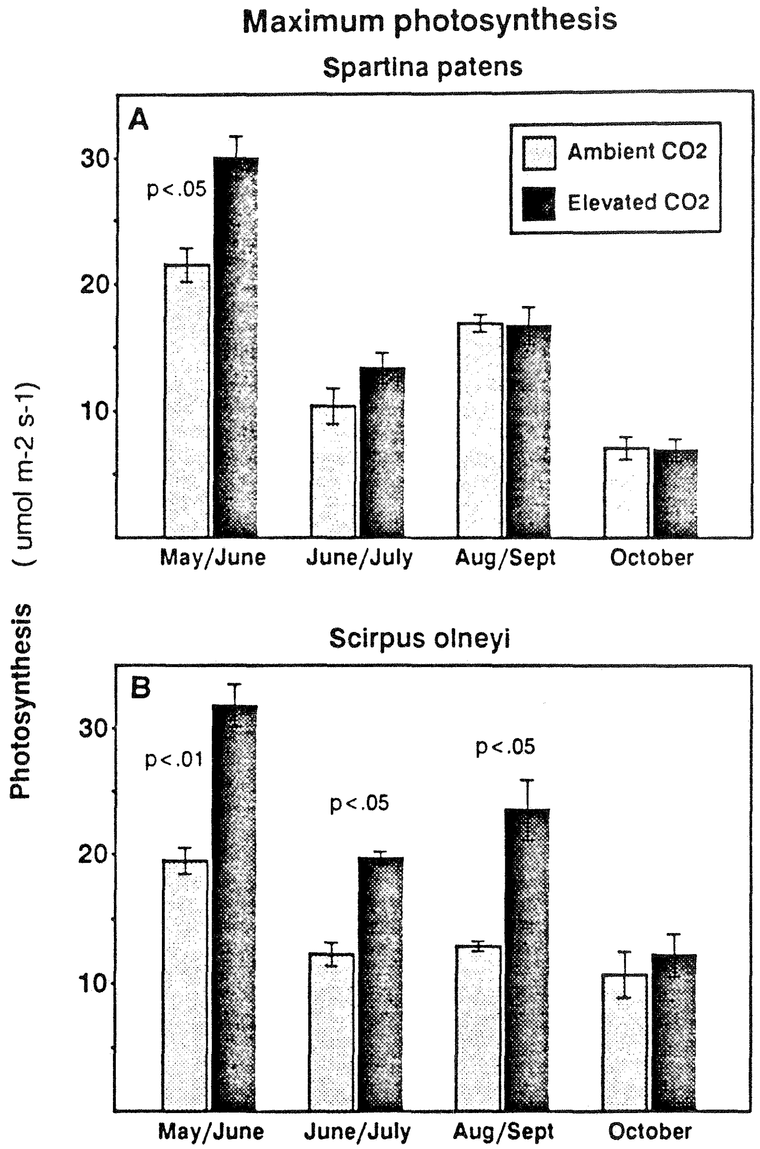


Figure 4.3. Maximum photosynthesis of *Spartina patens* leaves (A) and *Scirpus olneyi* stems (B) grown and measured at ambient CO_2 (light bars) or grown and measured at elevated CO_2 (dark bars) for four periods during the 1988 growing season.

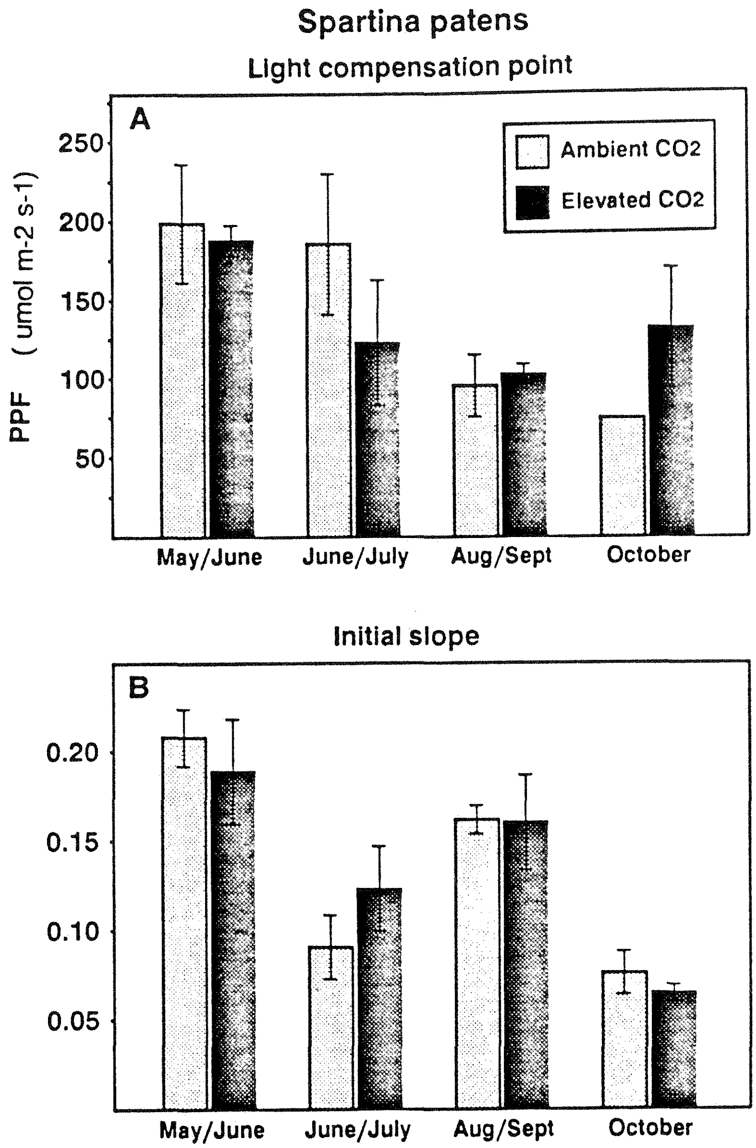


Figure 4.4. Mean light compensation points (A) and initial slopes (B) of light response curves of *Spartina patens* during the 1988 growing season. Light bars represent plants grown and measured at ambient CO_2, dark bars signify plants grown and measured at elevated CO_2.

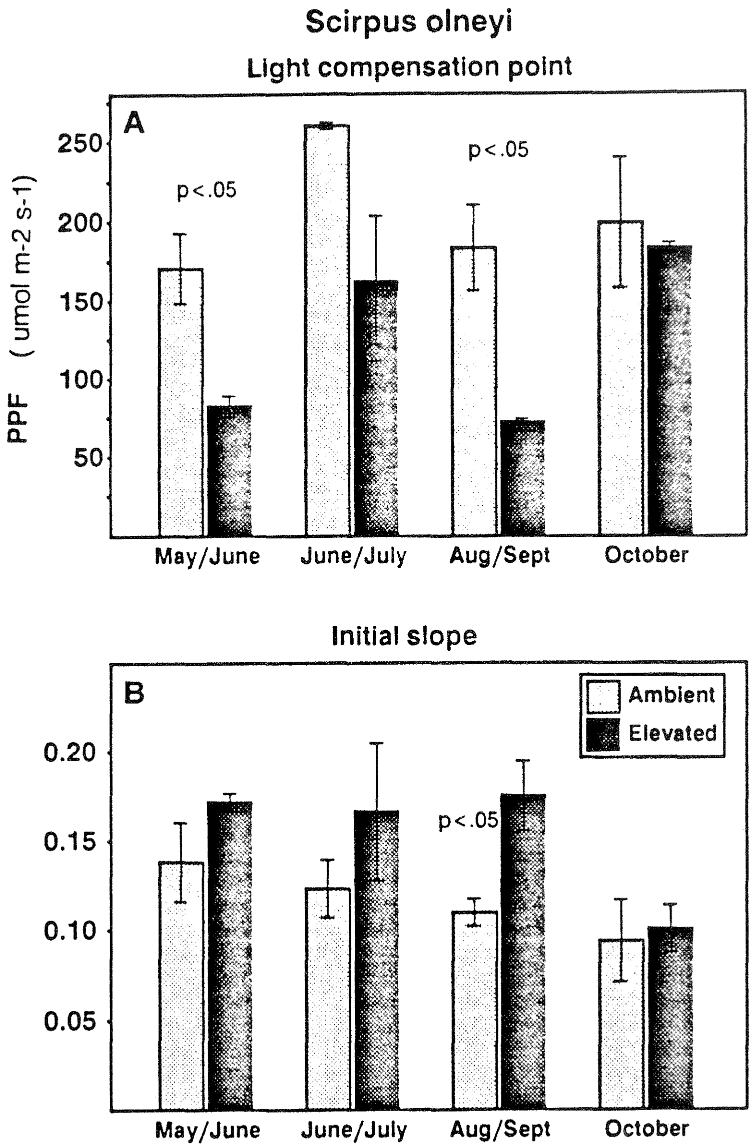


Figure 4.5. Mean light compensation points (A) and initial slopes (B) of light response curves of *Scirpus olneyi* during the 1988 growing season. Light bars represent plants grown and measured at ambient CO_2, dark bars signify plants grown and measured at elevated CO_2.

Chapter 5. Canopy CO_2 exchange.

This chapter deals with the daytime carbon uptake and nighttime carbon loss on a canopy basis. A carbon budget for 1988 based on the carbon exchange data is presented, and a comparison is made between the carbon budget and the estimated amount of carbon in above and belowground biomass.

Photosynthesis

methods.

By converting the open top chambers to closed top chambers by placing a lid with a restricted opening on the chambers, carbon and water exchange in the chambers could be measured. Absolute CO_2 concentrations and the difference in CO_2 concentration between air entering the chamber and air exiting the chamber was measured using a BINOS infra-red gas analyzer. Closed tops were put on chambers of one community at a time and were changed to a new community after at least one complete 24 hour carbon exchange measurement had been made. With ten closed chambers it was possible to measure each chamber every eight to ten minutes. Canopy carbon exchange measurements were made from mid May until mid November.

A detailed description of the gas circuit and the methods used for canopy carbon exchange measurements is given in greenbook #038 and #044 and in Drake et al. (1989).

Results

A set of 24 hour carbon exchange curves is shown in figure 5.1 (Scirpus community), figure 5.2 (Spartina community) and figure 5.3 (Mixed community) for ambient and elevated chambers for three periods during the growing season.

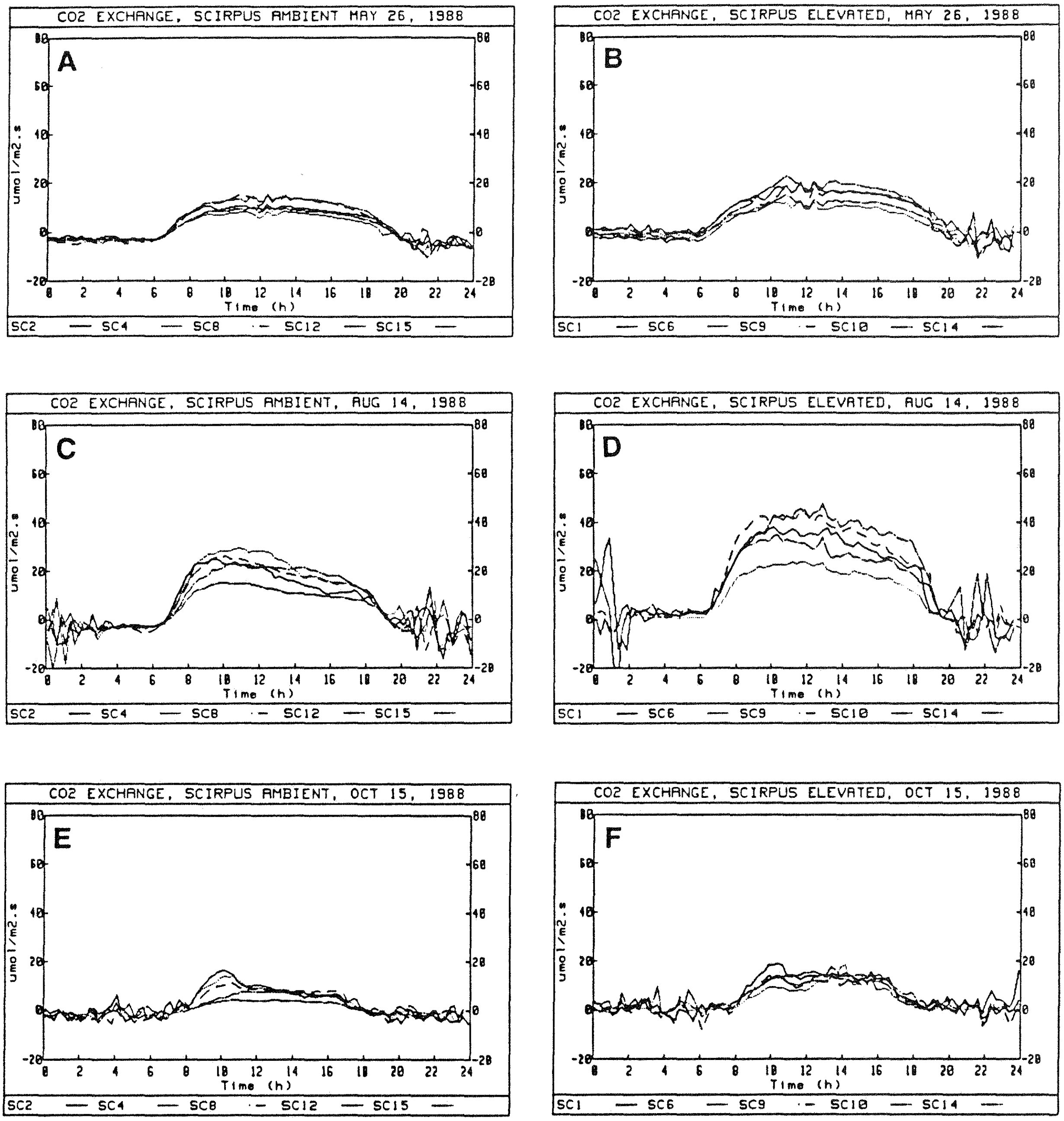


Figure 5.1. Canopy CO_2 exchange of the *Scirpus* community over a 24 hour period for five ambient and five elevated chambers. CO_2 exchange is shown for three days in the 1988 season: A day at the beginning of the growing season (A and B), a day in the period of peak standing biomass (C and D) and a day late in the season (E and F). CO_2 exchange is expressed in μmol CO_2 per meter square ground area per second.

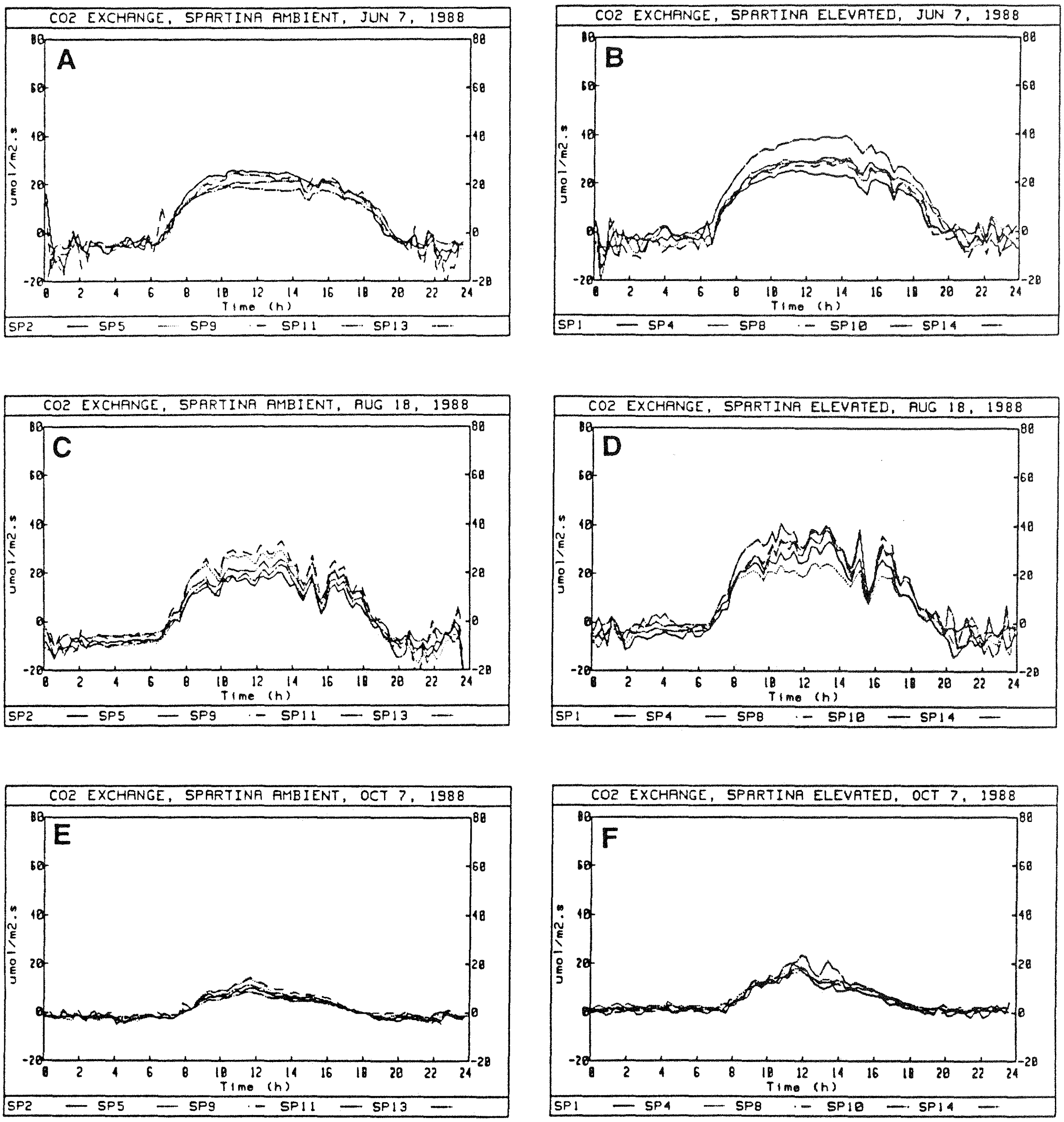


Figure 5.2. Canopy CO_2 exchange of the *Spartina* community over a 24 hour period for five ambient and five elevated chambers. CO_2 exchange is shown for three days in the 1988 season: A day at the beginning of the growing season (A and B), a day in the period of peak standing biomass (C and D) and a day late in the season (E and F). CO_2 exchange is expressed in μmol CO_2 per meter square ground area per second.

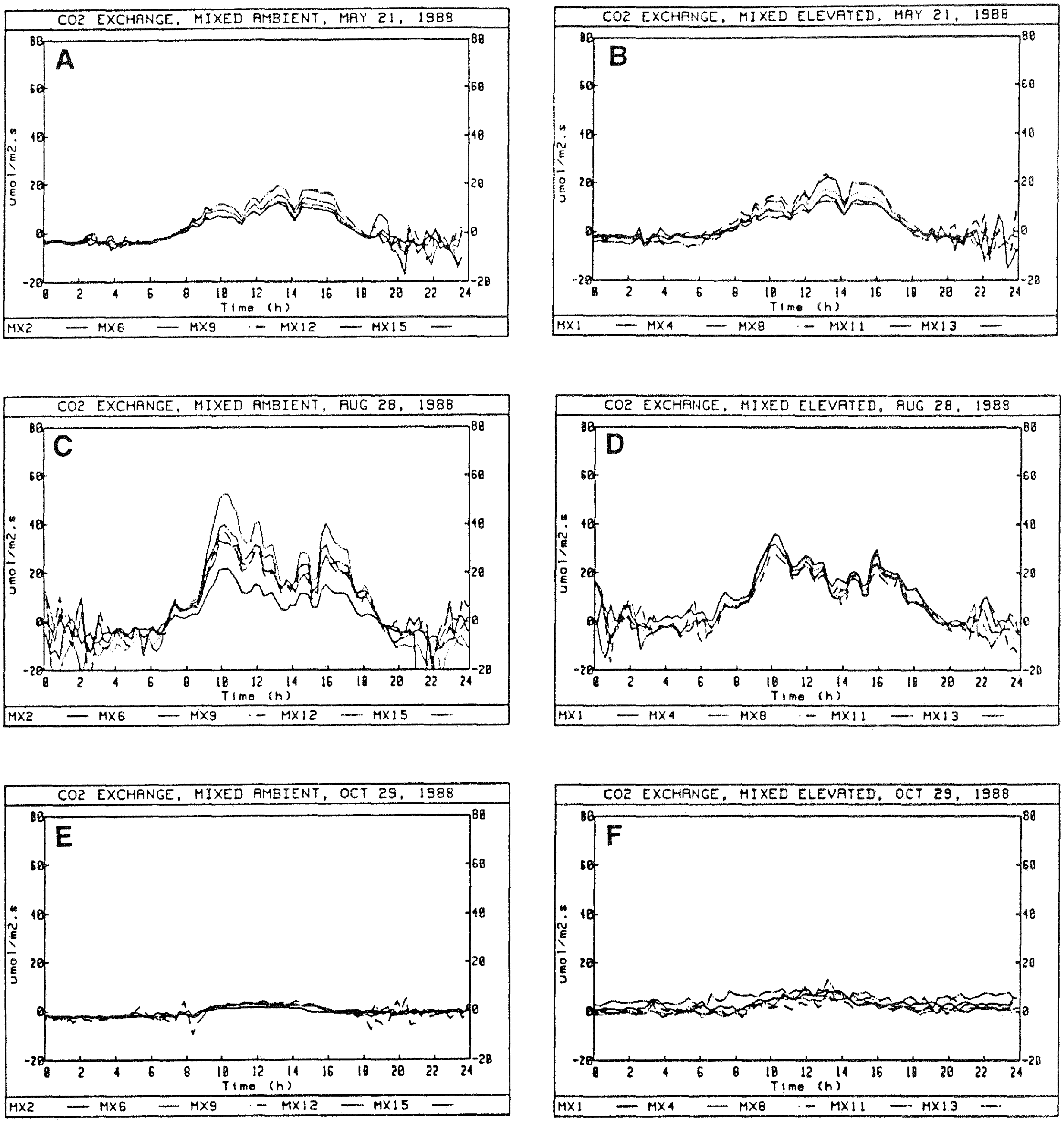


Figure 5.3. Canopy CO_2 exchange of the Mixed community over a 24 hour period for five ambient and five elevated chambers. CO_2 exchange is shown for three days in the 1988 season: A day at the beginning of the growing season (A and B), a day in the period of peak standing biomass (C and D) and a day late in the season (E and F). CO_2 exchange is expressed in μmol CO_2 per meter square ground area per second.

Panels A and B of figure 5.2, 5.2 and 5.3 represent a day at the beginning of the season, panels C and D show a day in the period of peak standing biomass and panels E and F show a day at the end of the season.

In figure 5.4 the total daytime carbon uptake throughout the season is shown for all three communities. Total daytime carbon uptake is the accumulated CO_2 uptake in a chamber from sun up to sun down. The mean and standard error of five chambers are shown. The right hand side of the figure (panel B, D and F) shows the percent increase in carbon uptake in an elevated chamber as compared with an ambient chamber. The data shown are the means and standard error of five chamber pairs. A more detailed presentation of the data is given in table 5.1 (Scirpus), 5.2 (Spartina) and 5.3 (Mixed), with the daytime carbon uptake for each chamber and data on light and temperature.

Carbon uptake in the *Scirpus* community is greatly enhanced by elevated CO_2, showing an average 80 % improvement during the months June, July and August, the period of maximum carbon uptake. The *Spartina* community responded to elevated CO_2 with an average 30% increase in canopy carbon uptake. The response to elevated CO_2 was largest at the beginning and at the end of the growing season. The mixed community showed the least increase to elevated CO_2 with an average 13% improvement.

Because of these differences in response to elevated CO_2, the carbon uptake of the *Scirpus* community, which was lower than the *Spartina* and the mixed community at ambient CO_2, was as high as the carbon uptake of the mixed community and higher than the *Spartina* community at elevated CO_2.

Maximum daytime carbon uptake rates were reached in June and July, approximately a month before the period of peak standing green biomass. This can be explained by the longer light periods early in the season, the higher photosynthetic capacity of younger leaves and the absence of self shading.

The elevated chambers continued with daytime carbon uptake at the end of the season when carbon uptake in the ambient chambers had already stopped. This could be due to an effect of elevated CO_2 on senescence even though no difference in the percent senescent tissue between treatments was found (chapter 2).

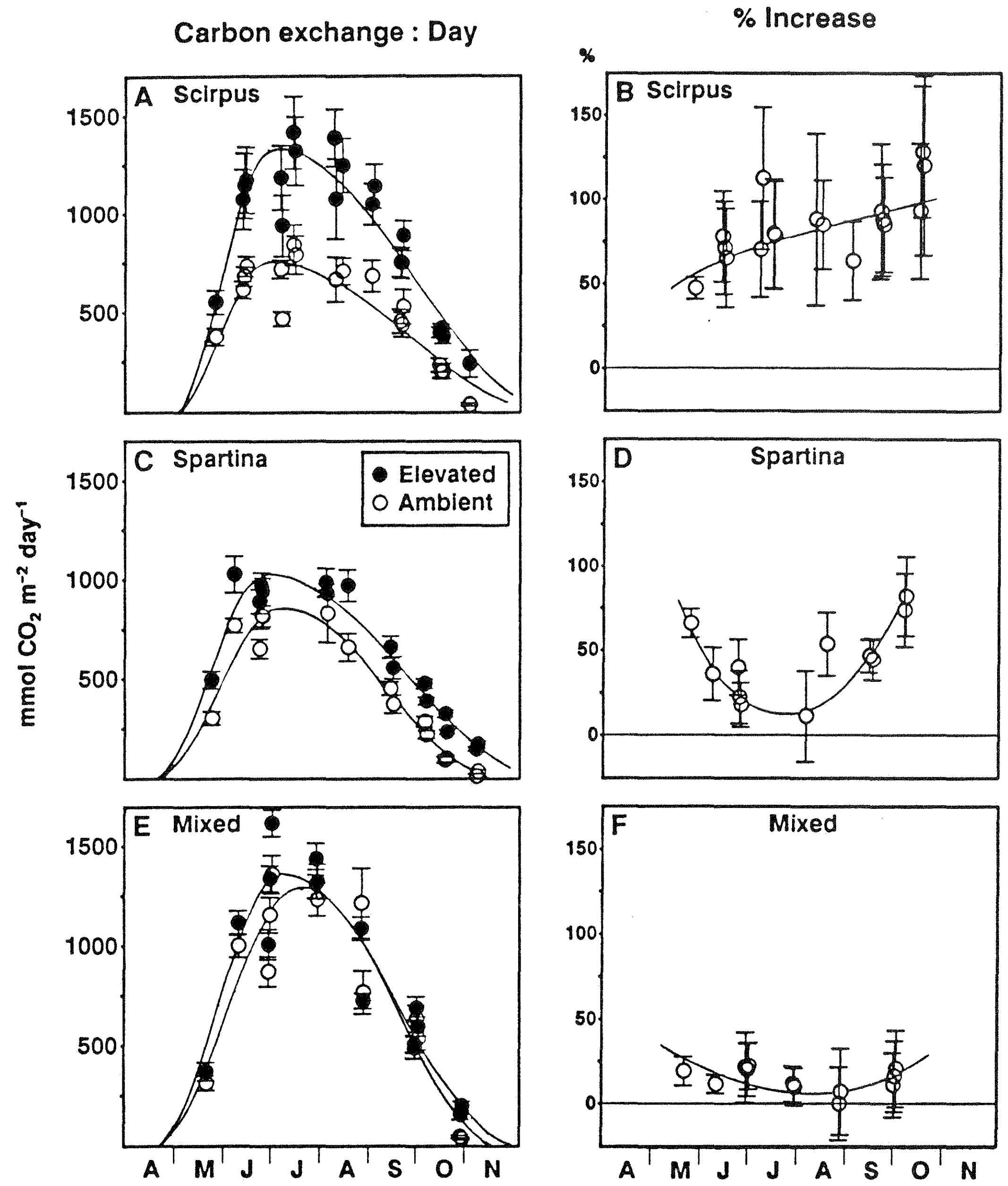


Figure 5.4. Total daytime carbon uptake of the *Scirpus* (A,B), *Spartina* (C,D) and mixed (E,F) community during the growing season 1988. Panels A, C and E show the mean values and standard error of five ambient and five elevated chambers. Panels B, D and F show the percent increase in daytime carbon uptake due to elevated CO_2. Mean and standard error of five chamber pairs.

The relative effect of elevated CO_2 on daytime carbon uptake of the *Scirpus* community per unit ground area increased throughout the season (figures 5.4.B, 5.5). This increase can be explained by the effect of elevated CO_2 on the amount of green biomass per unit ground area (figure 5.5). Early in the season the biomass was higher in the ambient chambers, while at the end of the season there was 30% more green biomass in the elevated chambers. If the data are expressed as percent increase in daytime carbon uptake per unit green biomass then the effect of elevated CO_2 was a constant 55% increase throughout the season.

In figure 5.6 the canopy photosynthesis at maximum light is shown for the three communities during the 1988 season. More data points were available for these graphs because they did not require a complete daytime data set for each day. The seasonal trend of photosynthesis at maximum light and the effect of elevated CO_2 is very similar to the total daytime carbon uptake (figure 5.4).

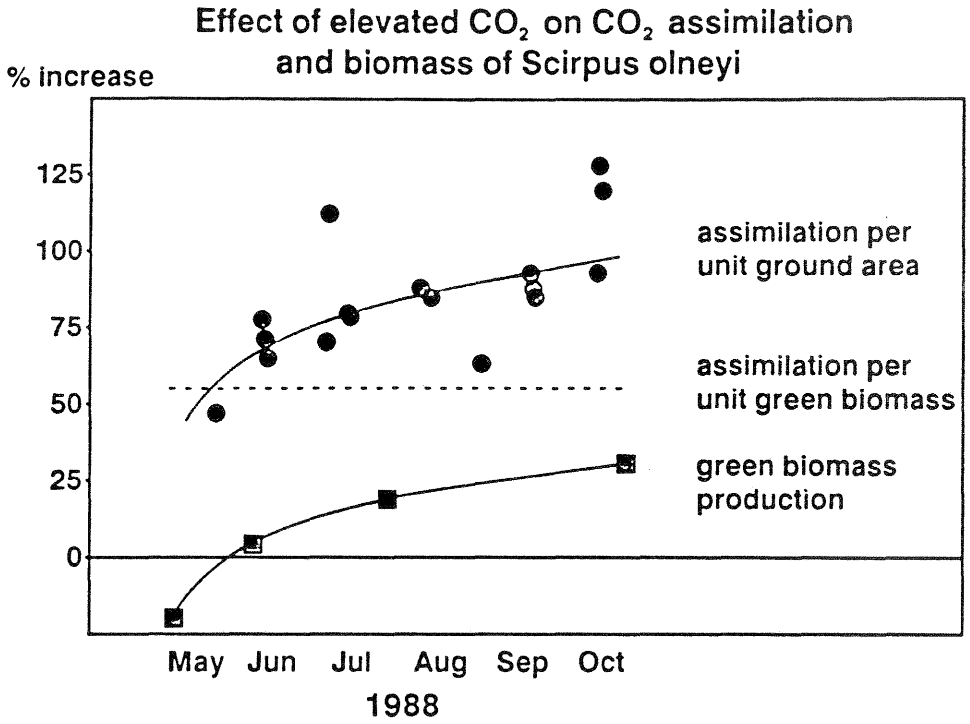


Figure 5.5. The effect of elevated CO_2 (as percent increase) on total daytime carbon uptake of the *Scirpus* community (circles), and on green biomass (squares) during the growing season. Values are means of five chambers. The dotted line represents the effect of elevated CO_2 on daytime carbon uptake per unit green biomass.

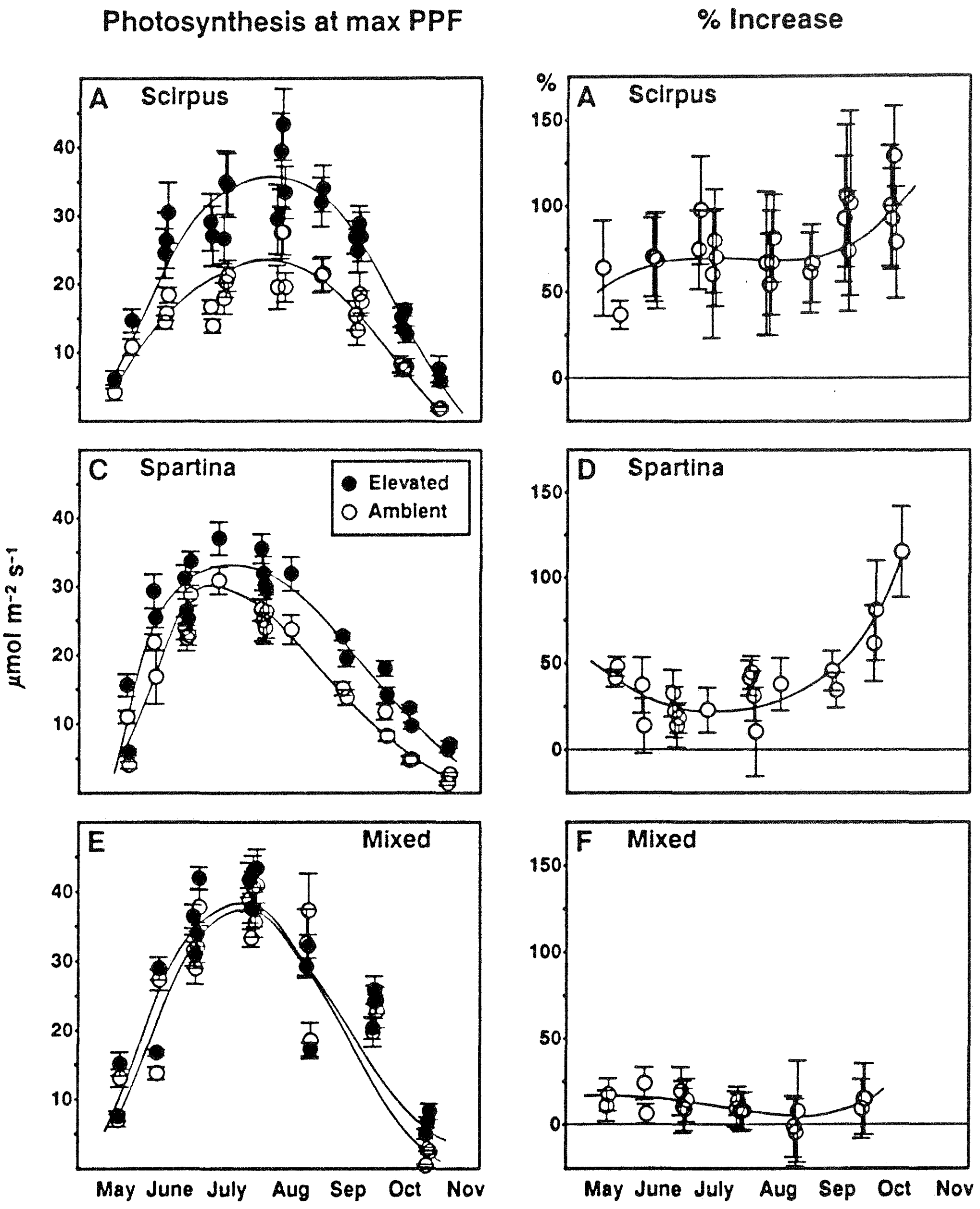


Figure 5.6. Carbon uptake at maximum light of the *Scirpus* (A,B), *Spartina* (C,D) and mixed (E,F) community during the growing season 1988. Panels A, C and E show the mean values and standard error of five ambient and five elevated chambers. Panels B, D and F show the percent increase in carbon uptake due to elevated CO_2. Mean and standard error of five chamber pairs.

Dark respiration and decomposition.

The effects of elevated CO_2 on dark respiration of plants have been studied less than most other physiological responses and the available data indicate no clear pattern as to whether dark respiration increases or decreases compared to respiration of plants grown in normal ambient CO_2. In this chapter the effect of elevated CO_2 on respiration of a salt marsh canopy and of single leaves of a wide variety of species are presented.

canopy respiration

Nighttime canopy gas exchange measurements provided data for canopy dark respiration. Frequently very high and highly fluctuating ambient CO_2 concentrations were observed during the night. These conditions interfered with canopy gas exchange measurement, limiting the number of valid respiration measurements. Because the CO_2 concentration was most unstable close to the marsh surface, the air inlet for the chambers was changed from one to three meters above the marsh. Net ecosystem respiration was reduced by elevated CO_2 in all three communities (figure 5.7). The effect of elevated CO_2 increased during the season suggesting that age of leaves is an important variable.

Single leaf respiration

To confirm the effect of elevated CO_2 on dark respiration on canopy level, dark respiration was measured on single leaves of *Scirpus* and *Spartina* grown at ambient and elevated CO_2 in a greenhouse at the USDA in Beltsville, Maryland. Plants were grown in large pots in closed top chambers and received supplemental lighting to give 18.4 mol m^{-2} day^{-1}. Plants were grown at 24.8 °C, mean minimum, 32 °C, mean maximum, 28 °C temperature during measurement, and CO_2 concentrations of 370 (ambient) and 720 ppm (elevated). Because elevated CO_2 might affect respiration in two ways, by changing the tissue composition of plants grown in elevated CO_2, and

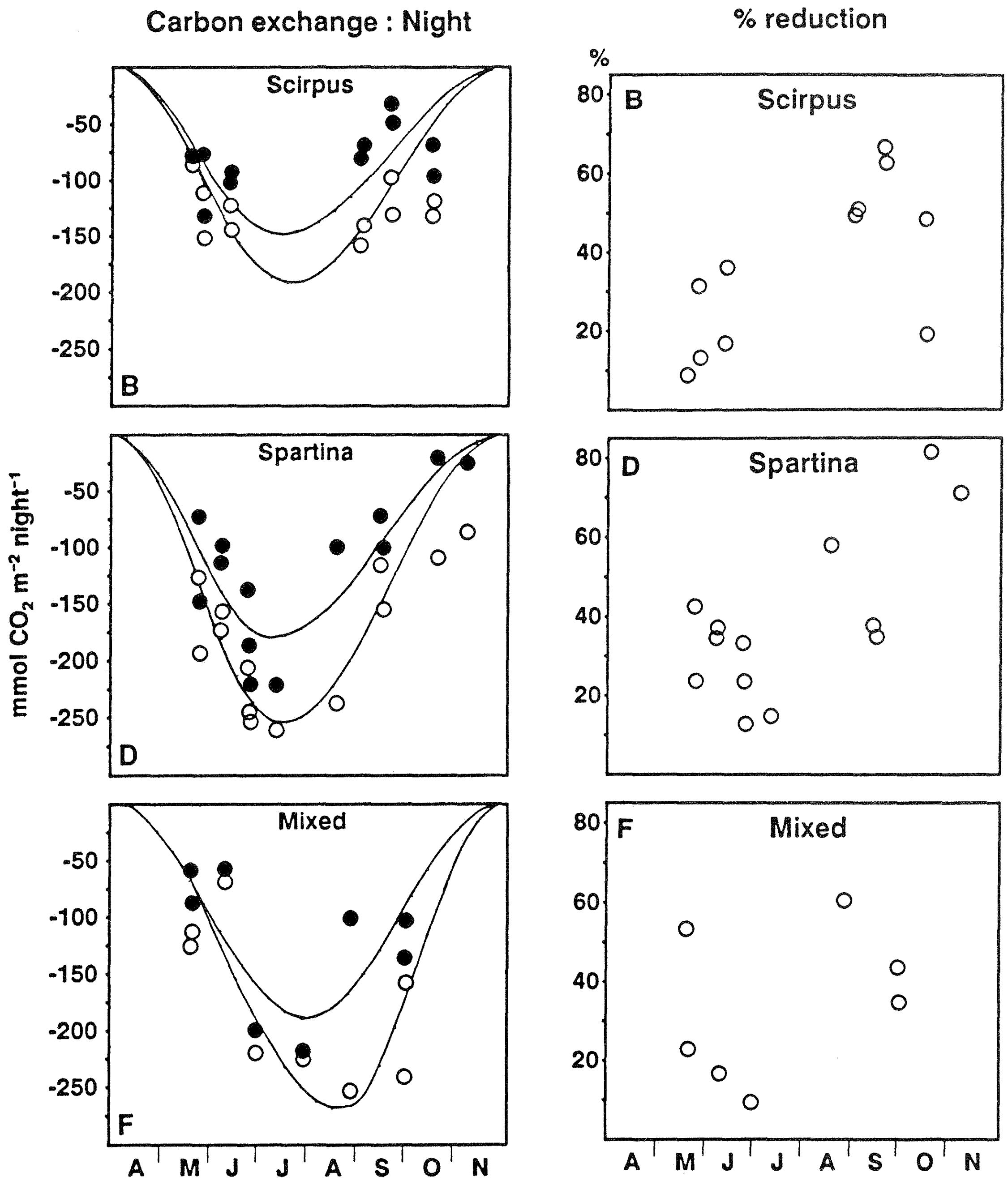


Figure 5.7. Canopy night-time CO_2 exchange for the three communities during the 1988 season (A, C and E). The effect of elevated CO_2 on respiration expressed as percent reduction is shown in B, D and F.

by affecting the respiration at the time of measurement, dark respiration was measured at both ambient and elevated CO_2. The results are presented in figure 5.8. An elevated CO_2 concentration at the time of measurement reduced the dark respiration in both *Scirpus* and *Spartina* when compared with plants measured at ambient CO_2. The CO_2 concentration during growth did not affect the respiration rate of *Scirpus*, while *Spartina* showed an apparent acclimation by increasing the respiration rate of plants grown at elevated CO_2, almost canceling the reduction in respiration by elevated CO_2 at the time of measurement.

In order to find out if the reduction of dark respiration by elevated CO_2 is a general phenomenon in plants, the effect of elevated CO_2 on respiration of several other species was measured. The species selected included temperate and tropical species, wild plants and crops, C_3 and C_4 species.

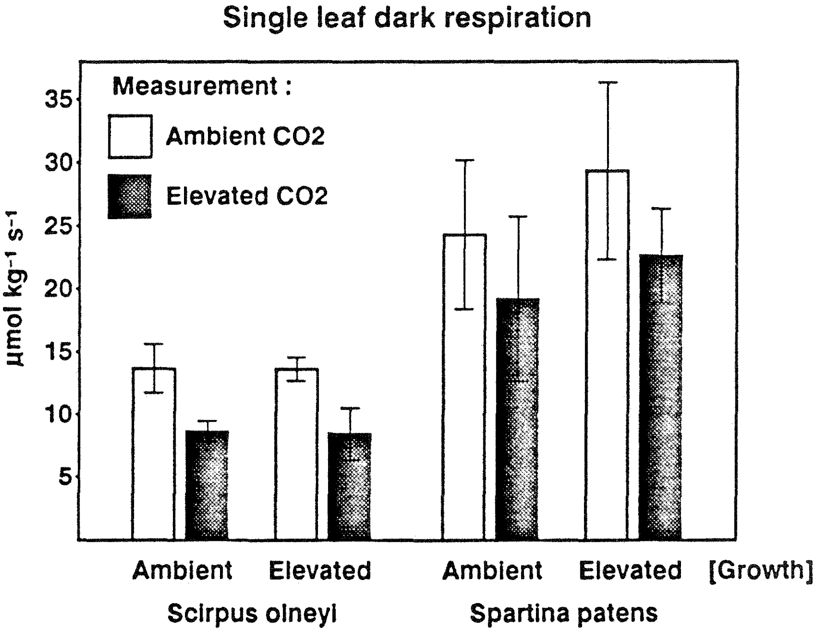
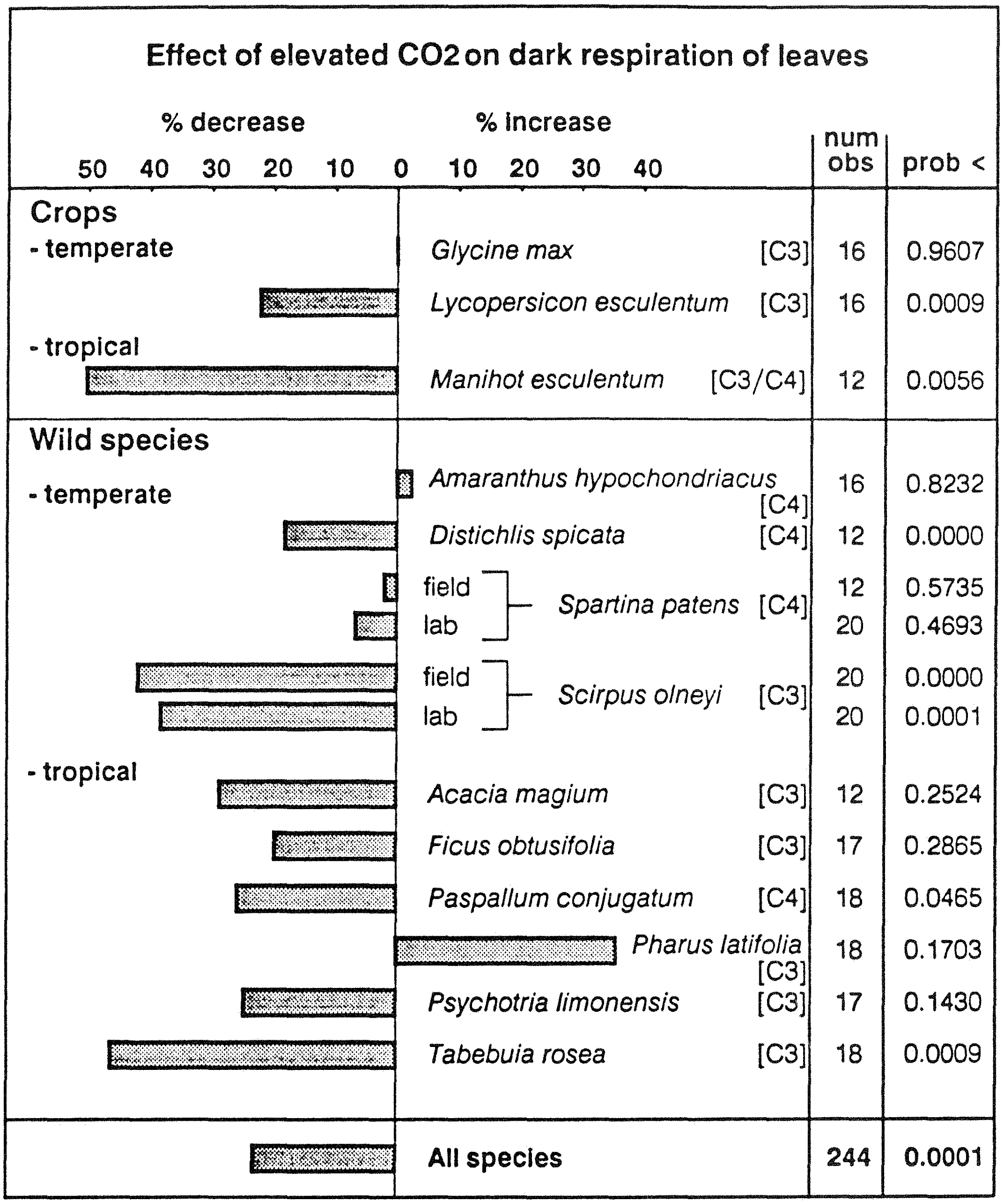


Figure 5.8. Single leaf dark respiration of *Scirpus* and *Spartina* plants grown in a controlled environment at elevated and ambient CO_2. Light bars show the mean respiration and standard error of plants measured at ambient CO_2, dark bars represent plants measured at elevated CO_2.

Dark respiration was measured in leaves and shoots of *Glycine max*, *Lycopersicon esculentum*, and *Amaranthus hypochondriacus* grown in elevated and normal ambient CO_2 in a greenhouse at the USDA in Beltsville, Maryland. Respiration was reduced in *Lycopersicon esculentum* but not in the other two species (Figure 5.9).

Seven tropical species were tested for the effect of elevated CO_2 on dark respiration. Plant material was collected in the field on Barro Colorado Island, Republic of Panama, transplanted to large pots in a screened growing house near the collecting site and exposed to normal ambient CO_2 or elevated CO_2. After aproximately 60 days, respiration rate of leaves was lower in elevated CO_2 in 6 of 7 species and higher in one, the grass *Pharis latifolia* (Figure 5.9). The range of the response of respiration of leaves to elevated CO_2 varied from a decrease of 50% in *Manihot esculentum*, to an increase of 35% in the grass, *Pharis latifolia*. CO_2 reduced respiration in both C_3 and C_4 species.

Although the effect of elevated CO_2 on respiration was not consistent in all species tested, when the data for the twelve species was pooled the effect was highly significant. Thus, in leaves and in ecosystem measurements growth in elevated CO_2 appears to reduce whole tissue dark respiration. Increased CO_2 could lead to reduced loss of carbon from the ecosystem. Ecosystem gas exchange measurements show that the effect of elevated CO_2 on respiration decreases carbon loss and results in increased carbon accumulation in the rhizospere.



			num obs	prob <
Crops				
- temperate	*Glycine max*	[C3]	16	0.9607
	Lycopersicon esculentum	[C3]	16	0.0009
- tropical	*Manihot esculentum*	[C3/C4]	12	0.0056
Wild species				
- temperate	*Amaranthus hypochondriacus*	[C4]	16	0.8232
	Distichlis spicata	[C4]	12	0.0000
	field — *Spartina patens*	[C4]	12	0.5735
	lab — *Spartina patens*	[C4]	20	0.4693
	field — *Scirpus olneyi*	[C3]	20	0.0000
	lab — *Scirpus olneyi*	[C3]	20	0.0001
- tropical	*Acacia magium*	[C3]	12	0.2524
	Ficus obtusifolia	[C3]	17	0.2865
	Paspallum conjugatum	[C4]	18	0.0465
	Pharus latifolia	[C3]	18	0.1703
	Psychotria limonensis	[C3]	17	0.1430
	Tabebuia rosea	[C3]	18	0.0009
	All species		**244**	**0.0001**

Figure 5.9. The effect of elevated CO_2 on dark respiration of leaves of a variety of species. A decrease in respiration is shown as a bar extending to the left, while a bar extending to the right signifies an increase in respiration. For each species the photosynthtic pathway, the number of observations and the level of significance is given. Data for respiration of *Scirpus olneyi* and *Spartina patens* in the field were obtained during the summer of 1989.

Decomposition

Growth in elevated CO_2 affects the composition of plant tissues (see chapter 3), which in turn may alter the decomposition rate of the dead plant material. It is also possible that the decomposition is influenced directly by the CO_2 concentration.

To quantify the the microbial respiration dead plant material of *Scirpus olneyi* and *Spartina patens* was collected from ambient and elevated chambers and from control sites. Fifteen samples were collected from each species, three treatments and five replicates. Plant material was collected in august 1988 and in January 1989 for two seperate experiments. Samples were divided in half to allow for incubations in both ambient and elevated CO_2. Dead plant material was incubated in 50 ml syringes. After an appropiate incubation time (depending on the moisture and the quantity of the sample), 10 ml air samples were extracted from the incubation syringe and injected into a system using an IRGA to measure carbon dioxide. The values were compared to a standard curve and the mg C kg^{-1} h^{-1} for each sample was calculated. The temperature during incubation was 24 °C for the August 1988 experiment and 3.5 °C for the experiment in January 1989.

The results are shown in figure 5.10.A for August 1988 and in 5.10.B for January 1989. The data for August 1988 show a significant decrease of microbial respiration for *Scirpus* grown in elevated CO_2. The CO_2 concentration during the incubation did not affect the decomposition rate. No significant effects were found for *Spartina* tissues. The January values did not exhibit significant differences. This is most likely because of the low temperature during incubation and the variability in moisture levels of the plant material collected. The January samples were all very wet due to the extremely heavy rain during the day that the material was collected.

The results of these two experiments are inconclusive. During 1989 we have repeated this preliminary experiment and the results will be reported in the next greenbook.

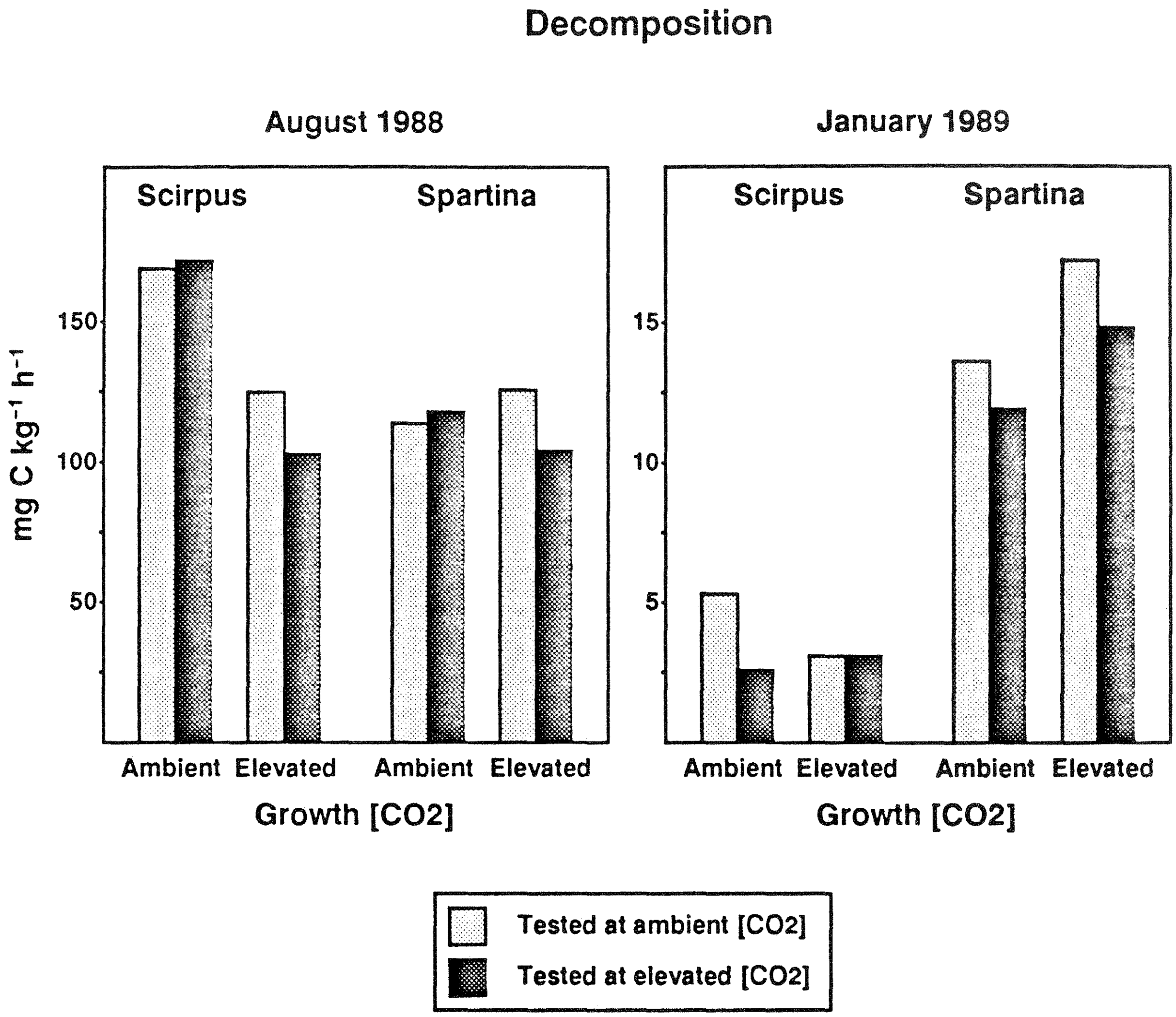


Figure 5.10. Microbial respiration rates of dead plant material of *scirpus olneyi* and *Spartina patens* grown in ambient and elevated CO_2. Plant material was incubated at both CO_2 concentrations. Results are shown for material collected in August 1988 (A) and January 1989 (B). Temperatures during measurement were 24 °C for August 1988 and 3.5 °C for January 1989.

Carbon budget 1988.

The carbon budget for 1988 consists of an estimation of total net carbon uptake by the communities for one growing season. The carbon uptake by photosynthesis and the carbon loss by respiration can be estimated from the canopy carbon exchange data. The difference between these two numbers is the net seasonal carbon uptake. The carbon budget will be compared with the amount of carbon stored in above and belowground biomass. The amount of carbon accumulated in aboveground biomass can be calculated using the total biomass data from the vegetation sensuses and the percent carbon in the plant tissue as measured in the CHN analysis. The element of the carbon balance that is not readily available is the amount of carbon stored belowground. The original root cores provide us with data concerning the rhizome biomass in the top 20 cm of the soil but give little information about roots, while the regrowth cores underestimate the total biomass of the roots and rhizomes. No information is present on the biomass of roots penetrating more than 20 cm into the marsh.

Seasonal carbon uptake.

Canopy carbon uptake was measured in all communities at regular intervals during the 1988 growing season. Since the measurements were not continuous throughout the season the carbon uptake had to be estimated for those times that no measurements were made. This was done by using a simple model describing the total daily carbon uptake as a function of Julian day. The parameters used in the model were a] first day with positive carbon uptake, b] day of maximum carbon uptake, c] last day with positive carbon uptake, and d] maximum carbon uptake. The model returned a zero value if the julian day was less than the first day or more than the last day, and uses a sine function to fit the data between the first day and the day of maximum carbon uptake and between this day and the last day. A least squares curve fitting routine was used to find the values of the parameters a,b,c and d.

A simple model describing daytime carbon uptake in 1988

```
if (day<a) or (day>c) then uptake=0;
else
  if day<b then mid=(a+b)/2 else mid=(b+c)/2;
  uptake = d/2 * (1 - sin((day-mid)/(b-mid)*pi/2));
```

where :

a = first day with positive carbon uptake (julian day)
b = day of maximum carbon uptake (Julian day)
c = last day with positive carbon uptake (Julian day)
d = maximum daytime carbon uptake (mmol $m^{-2}.day^{-1}$)
day = day for which carbon uptake is to be calculated. (Julian day)
uptake = estimated daytime carbon uptake for 'day'. (mmol $m^{-2}.day^{-1}$)

The total daytime carbon uptake was calculated for all days for which a complete dataset was available, and these data (the means of 5 chambers) were used to fit the model. Very few data points were found in the first few months of the growing season. Because this could cause an inaccurate estimation of the first day with positive carbon uptake, this day was arbitrarily set to be the same as the first day at which green biomass was present, making it into a three parameter model. The starting day for *Scirpus* (Julian day 120) is later than the starting day for *Spartina* and mixed (Julian day 108) because *Spartina* shoots emerged approximately two weeks earlier. Including mean daytime temperature or total light during the daytime period into the model did not improve the goodness of fit.

The total amount of carbon absorbed during the 1988 season is calculated by summing the predicted total daytime carbon uptake for each day in the season. The integrated values for the ambient and elevated chambers and the values of the parameters for the best fitting curves are given in table 5.4. The best fitting curves are shown in figure 5.4, along with the original data points. Elevated CO_2 increased the total seasonal carbon uptake in *Scirpus* by 79%, in *Spartina* by 38%, and in the mixed community by 10%.

The carbon uptake in the C_4 dominated mixed community was already very high at ambient CO_2 and elevating the CO_2 concentration resulted in only a small increase. The carbon uptake in the pure C_4 community was much lower at ambient CO_2 and raising the CO_2 concentration significantly increased the carbon uptake. A possible explanation is that during the relatively dry season of 1988 *Spartina* in the pure community experienced drought stress which reduced carbon uptake and which was relieved by elevated CO_2. The mixed community has a slightly lower elevation than the *Spartina* community, which could enable the roots of the C_4 plants to reach the soil water table, preventing drought stress, and allowing a near optimum carbon uptake. In this case elevated CO_2 is expected to improve only the carbon uptake of the C_3 species, which constitutes a minor segment of the mixed community.

Seasonal carbon loss.

An identical method is used for calculating the nighttime CO_2 loss. Difficulties in measuring the ecosystem CO_2 loss at night were responsible for the absence of nights with a complete set of good respiration data. Therefore sections of the night were selected which provided reasonable data and a total dark period carbon loss was extrapolated from these numbers.

The small number of data points and the high variability in the data over the season made it necessary to select a starting and ending date for the respiration season. The dates selected were April 1st and December 1st, the selection was based on information from Drake and Read (1981). The model was the same as the one used for total daytime carbon uptake, and the total amount of carbon lost to respiration was calculated by summing the predicted total nighttime respiration values for all nights in the season.

The estimated values and the parameter values for the best fitting curves are presented in table 5.5. The data points used in the models and the best fitting curves are shown in figure 5.7. The model for *Spartina* fit the data reasonably well. The lack of good respiration data for *Scirpus* during the mid part of the season it was assumed that respiration of *Scirpus* followed the same pattern through the season as *Spartina*. Total seasonal carbon loss was reduced at elevated CO_2 by 23% in *Scirpus*, 29% in *Spartina* and 30% in the mixed community.

Figure 5.11.a shows the carbon budget for the three communities based on the canopy gas exchange data. In all cases elevated CO_2 increases the daytime carbon uptake and decreases the nighttime carbon loss, resulting in a enhanced effect on net carbon uptake. The effect of elevated CO_2 as percent increase in daytime carbon uptake, nighttime carbon loss and net carbon uptake for the three communities is shown in figure 5.11.b.

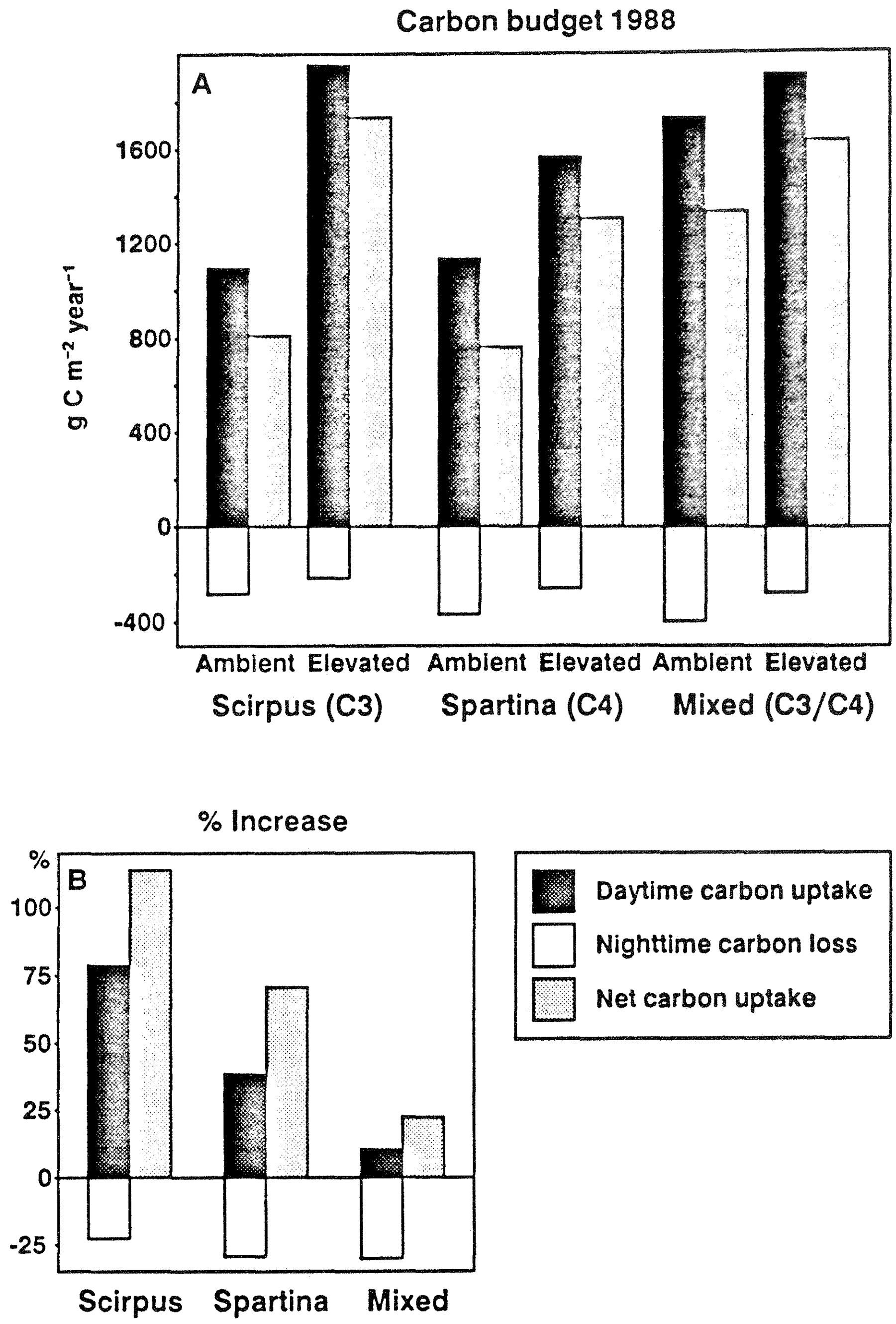


Figure 5.11. A. Total seasonal daytime carbon uptake, night-time carbon release and net carbon gain for the three communities during the 1988 season. Units in gram carbon per meter square per year. B. The effect of elevated CO_2 as a percent increase of carbon uptake, carbon loss and net carbon gain of the three communities.

Carbon stored in aboveground biomass

In the CHN analysis (see chapter 3) the carbon content of plant material for different harvests, species and treatments was determined. The percentage of carbon in *Scirpus* shoots and *Spartina* leaves from the pure communities are shown in figure 5.12. Information for other tissues and for the mixed community can be found in table 5.7. The carbon content of plants grown in control sites appears to be higher than the carbon content of ambient grown plants for *Scirpus* and *Spartina*. This points to a chamber effect lowering the carbon content. Elevated CO_2 increased the percent carbon in these plants, although not quite compensating the chamber effect. These effects are small but appear to be consistent, with the largest variations in carbon content in senescent tissue. No chamber or CO_2 effect on carbon content was found for *Spartina* stems, or for stems, leaves and senescent tissue of *Distichlis*.

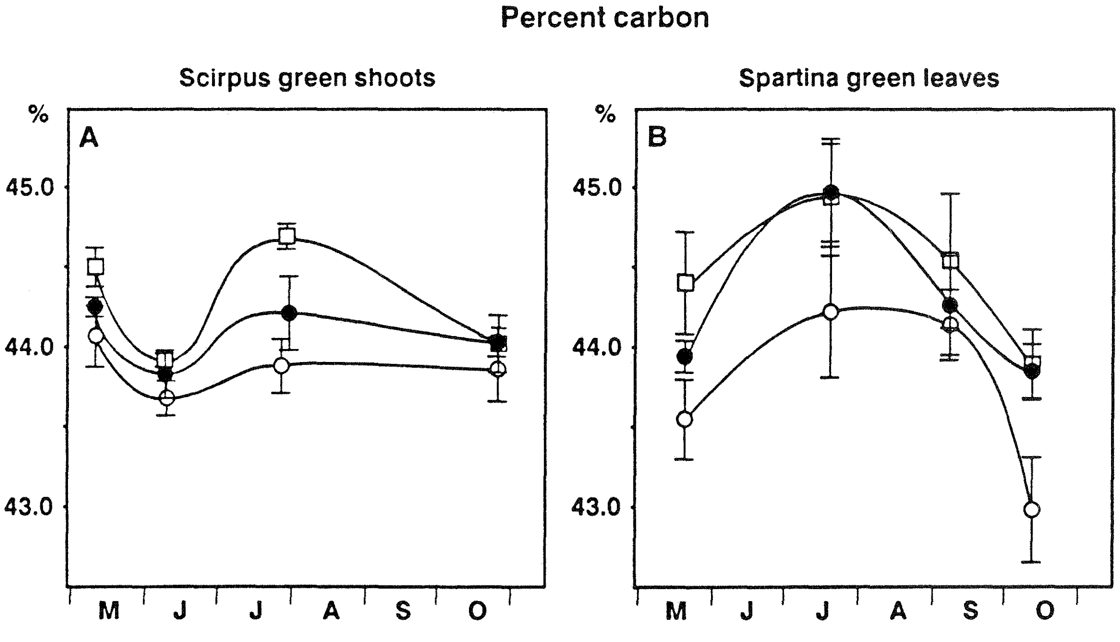


Figure 5.12. Percent carbon in Scirpus green shoots (A) and Spartina green leaves (B) at the four harvests of the 1988 season. Mean and standard error of five chambers.

Table 5.6 contains data on the total biomass, percent carbon and total carbon in g m^{-2} for senescent tissue, leaves and stems. The data presented are the means for five chambers at peak standing biomass. The data for the mixed community are given seperately for each species as well as for the combined species. Very little change in total aboveground carbon was found for the pure *Scirpus* and *Spartina* communities. In the mixed community the amount of carbon in *Spartina* declined by 7% while the carbon content of *Distichlis* and *Scirpus* increased by 50 % and 323 % respectively, leading to an overall 33 % increase in total aboveground carbon in the mixed community. This effect is mainly due to changes in aboveground biomass (*Spartina* -12 %, *Distichlis* +50 %, *Scirpus* +277 %), because the percent carbon in the plant tissues varied only slightly.

Carbon stored in belowground biomass.

No chamber or CO_2 effect was found on the carbon content of roots and rhizomes in regrowth cores (table 5.8). Belowground plant material from the original root cores were not analyzed for carbon and nitrogen. In table 5.9 the percent carbon, total biomass and total carbon are presented for roots and rhizomes from the regrowth cores. An accurate estimation of the belowground biomass and of the amount of carbon in roots and rhizomes is not possible because

A] Roots biomass cannot be estimated in original cores.

B] Regrowth cores only provide data on new growth, and may not be an accurate model for the marsh substrate.

C] The small core diameter and the limited number of samples prevent an accurate estimation of Scirpus rhizomes, which are sparse.

D] No information is available on roots and rhizomes below 20 cm.

The available information on belowground biomass consists of

A] Root growth was significantly increased by 63% in Scirpus regrowth cores (figure 2.12.B).

B] The rhizome biomass recovered from original cores was six (Spartina) to twelve (Scirpus) times higher than the rhizome biomass in regrowth cores (Table 2.7, 2.8).

C] Root biomass in Scirpus regrowth cores did not decrease with depth (fig 2.12), pre-dawn waterpotential data suggest that Scirpus roots may go down 50 to 100 cm (chapter 6, figure 6.8).

These data suggest that the belowground biomass is much larger than can be estimated from the regrowth cores, and may provide a sink for the carbon taken up by gas exchange.

A comparison of carbon uptake and carbon present in biomass.

Table 5.10 shows a comparison between the amount of carbon accumulated during the 1988 season, and the amount of carbon present in aboveground biomass. Because estimating the belowground biomass was not possible, for reasons given above, the capacity of the belowground biomass to act as a sink for carbon taken up by gas exchange remains unknown. Carbon escaping from the system as root turnover and root exudation, or in gaseous form (methane) is also not accounted for. A larger set of regrowth cores has been inserted into the marsh and will be harvested after two growing seasons. This may provide more information on the amount of belowground biomass and the effect of elevated CO_2.

							------------ Total daytime carbon uptake -----------						
Date	PPF Total	Mean Temp	Min Temp	Max Temp	N	treatment	block 1	block 2	block 3	block 4	block 5	Mean	StdErr
May 26	68.5	22.8	9.1	28.5	52	A	373.8	250.2	463.9	313.9	483.5	377.1	44.1
						E	634.0	376.4	612.3	439.9	690.7	550.7	60.4
Jun 12	58.9	29.5	12.2	36.9	57	A	609.0	567.4	764.1	506.3	613.5	612.1	42.6
						E	1114.3	591.8	1018.7	1071.7	1567.7	1072.8	155.1
Jun 13	55.4	32.2	16.5	39.0	56	A	710.0	634.2	832.2	545.4	678.7	680.1	47.1
						E	1101.0	645.7	1074.4	1207.8	1680.2	1141.8	165.3
Jun 14	52.6	33.6	17.0	40.5	55	A	777.0	716.1	887.2	577.8	700.1	731.6	50.6
						E	1130.8	667.6	1062.5	1281.5	1711.5	1170.8	169.0
Jul 06	49.5	32.7	17.1	40.5	56	A	737.0	771.4	812.5	551.0	709.6	716.3	44.8
						E	1096.7	663.9	1206.4	1260.7	1689.8	1183.5	164.4
Jul 07	53.6	34.7	19.2	40.9	54	A	439.6	553.1	525.3	341.5	464.1	464.7	36.9
						E	807.7	489.1	910.0	1036.4	1448.2	938.3	156.4
Jul 14	49.1	33.0	20.0	39.5	55	A	892.6	897.2	1153.9	542.5	709.3	839.1	102.5
						E	1375.7	785.5	1723.7	1352.1	1824.1	1412.2	182.3
Jul 15	52.8	34.3	24.0	39.3	56	A	806.2	835.5	1086.4	486.6	726.3	788.2	96.5
						E	1218.3	749.7	1606.7	1280.7	1745.4	1320.2	173.2
Aug 10	52.9	34.2	23.0	39.5	52	A	.	835.7	.	449.4	710.6	665.2	113.8
						E	.	720.1	833.6	1109.9	1638.7	1075.6	204.8
Aug 14	52.3	35.8	25.7	41.5	52	A	702.5	860.3	766.6	457.6	744.7	706.3	67.3
						E	1266.4	779.7	1488.2	1145.7	1548.2	1245.6	137.5
Sep 02	43.0	28.9	13.7	34.9	49	A	759.6	804.6	823.3	399.7	620.1	681.5	78.9
						E	1189.2	699.8	1246.3	902.5	1206.0	1048.8	106.5
Sep 20	25.6	29.9	22.0	37.3	47	A	545.9	504.4	556.1	235.4	425.6	453.5	59.2
						E	.	565.4	895.9	710.8	832.1	751.1	72.8
Sep 21	13.0	26.9	18.8	31.5	41	A	538.3	609.1	356.1	254.2	427.9	437.1	63.2
						E	937.9	570.5	576.7	750.4	911.4	749.4	78.6
Sep 22	40.3	27.1	15.4	33.0	46	A	678.8	658.9	666.8	276.1	359.3	528.0	86.9
						E	1101.1	775.0	1047.4	782.1	731.9	887.5	77.2
Oct 15	29.4	22.9	3.1	32.0	42	A	307.9	272.9	271.4	111.9	203.0	233.4	34.8
						E	460.3	317.5	380.4	377.8	448.7	396.9	26.1
Oct 16	13.7	24.7	5.9	31.4	35	A	246.7	256.2	247.8	102.2	161.1	202.8	30.5
						E	505.7	404.7	385.0	374.0	412.7	416.4	23.4
Oct 17	39.6	23.1	7.6	32.5	41	A	287.5	254.3	254.3	89.7	142.6	205.7	38.0
						E	491.2	259.9	392.2	362.7	382.3	377.7	36.9
Nov 03	25.0	18.1	3.1	26.3	39	A	26.9	58.6	49.7	14.7	40.9	38.2	7.9
						E	488.3	116.2	186.4	138.1	271.9	240.2	67.5
		Chamber numbers :				Ambient	2	4	8	12	15		
						Elevated	1	6	9	10	14		

Table 5.1. Total daytime carbon uptake by the *Scirpus* community during 1988 for all days for which a complete dataset is available. The daytime period is defined as the period in which the light level exceeds 50 μmol m^{-2} s^{-1}. Shown are the total amount of light during this period, the mean, minimum and maximum temperature, the number of observations, the total daytime carbon uptake for the five ambient (A) and five elevated chambers (E), and the mean and standard error of the five chambers. The chamber numbers correlated with the ambient and elevated chambers of each block is given at the bottom of the table. Units for light are mol m^{-2} day^{-1}, units for carbon uptake are mmol m^{-2} day^{-1}.

							---------- Total daytime carbon uptake ------------						
Date	PPF Total	Mean Temp	Min Temp	Max Temp	N	treat ment	block 1	block 2	block 3	block 4	block 5	Mean	StdErr
May 24	49.3	28.7	17.7	36.3	53	A	362.6	398.3	220.6	293.7	243.6	303.8	33.9
						E	497.4	654.2	418.9	500.2	408.9	495.9	43.9
Jun 07	56.8	34.6	21.7	39.9	55	A	845.6	778.2	834.8	751.8	640.4	770.2	36.8
						E	816.3	984.2	943.7	1367.1	1035.0	1029.3	91.9
Jun 23	40.7	34.9	25.4	42.9	57	A	680.0	661.5	813.0	571.6	543.8	654	47.4
						E	670.9	851.3	942.1	987.1	1001.6	890.6	60.9
Jun 24	47.8	29.0	19.6	35.4	57	A	880.3	841.8	1033.0	691.7	655.8	820.5	68.2
						E	719.9	929.0	1062.3	1073.1	1063.2	969.5	67.8
Jun 25	44.1	28.3	16.1	35.0	57	A	863.8	849.5	961.6	713.8	693.2	816.4	50.1
						E	692.0	896.2	1044.1	1031.9	1041.2	941.1	68.2
Aug 05	54.2	34.6	23.0	38.8	53	A	665.7	1122.7	.	.	703.3	830.6	146.5
						E	917.7	945.9	.	.	.	931.8	14.1
Aug 18	34.9	33.4	26.6	38.8	51	A	476.5	751.7	863.9	663.3	539.7	659.0	70.0
						E	864.7	718.1	1079.1	1155.2	1043.7	972.2	79.4
Sep 14	20.1	30.3	17.9	35.4	41	A	345.2	515.2	517.8	400.9	481.6	452.1	34.1
						E	459.0	632.2	745.8	713.1	750.5	660.1	54.6
Sep 16	41.1	24.7	10.1	32.5	47	A	289.9	480.2	443.0	247.4	411.1	374.3	45.0
						E	.	532.6	649.0	413.3	635.0	557.5	54.6
Oct 06	14.9	20.5	7.9	26.8	37	A	228.5	339.2	349.1	220.7	289.6	285.4	26.8
						E	413.0	498.1	453.0	561.7	457.4	476.6	25.2
Oct 07	7.9	15.4	5.3	20.2	38	A	196.0	251.0	276.1	167.2	220.3	222.1	19.3
						E	338.9	402.6	371.9	455.3	376.8	389.1	19.4
Oct 19	.	19.6	11.2	26.3	35	A	66.8	126.6	115.1	51.3	110.1	94.0	14.7
						E	254.5	311.1	333.5	354.5	365.2	323.8	19.6
Oct 20	13.8	19.2	5.8	25.6	35	A	78.7	145.2	122.6	51.6	110.9	101.8	16.5
						E	198.1	267.7	234.7	227.7	238.3	233.3	11.1
Nov 08	6.7	15.0	2.8	20.3	30	A	32.1	25.5	2.8	-29.8	24.5	11.0	11.3
						E	126.3	181.1	150.5	122.2	147.7	145.6	10.5
Nov 09	22.2	16.5	3.9	22.6	38	A	46.2	43.7	42.4	1.8	48.2	36.5	8.7
						E	155.1	223.9	111.9	167.4	194.4	170.5	18.8
		Chamber numbers :				Ambient	2	5	9	11	13		
						Elevated	1	4	8	10	14		

Table 5.2. Total daytime carbon uptake by the *Spartina* community during 1988 for all days for which a complete dataset is available. The daytime period is defined as the period in which the light level exceeds 50 μmol m^{-2} s^{-1}. Shown are the total amount of light during this period, the mean, minimum and maximum temperature, the number of observations, the total daytime carbon uptake for the five ambient (A) and five elevated chambers (E), and the mean and standard error of the five chambers. The chamber numbers correlated with the ambient and elevated chambers of each block is given at the bottom of the table. Units for light are mol m^{-2} day^{-1}, units for carbon uptake are mmol m^{-2} day^{-1}.

							------------ Total daytime carbon uptake -----------						
Date	PPF Total	Mean Temp	Min Temp	Max Temp	N	treatment	block 1	block 2	block 3	block 4	block 5	Mean	StdErr
May 21	41.3	24.7	17.0	32.6	54	A	220.8	384.1	401.8	236.9	321.6	313.0	37.0
						E	301.6	350.6	508.8	256.3	430.0	369.5	45.2
Jun 10	60.4	22.2	8.8	28.6	57	A	845.1	1071.1	1173.6	918.5	1004.1	1002.5	57.4
						E	1094.1	1086.7	1289.1	925.4	1175.5	1114.2	59.6
Jun 29	49.4	30.1	19.6	37.0	56	A	618.1	969.2	1025.1	782.7	967.8	872.6	75.7
						E	1246.0	991.5	842.8	863.5	1090.1	1006.8	74.8
Jun 30	49.8	25.7	13.0	32.9	55	A	844.9	1288.7	1343.6	1077.2	1217.7	1154.4	89.3
						E	1516.8	1313.8	1204.6	1194.1	1452.1	1336.3	64.8
Jul 01	53.1	25.3	10.7	32.0	56	A	1012.5	1499.2	1554.5	1288.8	1445.2	1360.0	97.5
						E	1784.7	1595.1	1502.8	1448.2	1751.1	1616.4	66.4
Jul 29	46.7	33.1	22.3	38.3	54	A	1179.1	1230.2	1590.0	1295.3	1260.7	1311.1	72.3
						E	1591.9	1432.8	1259.7	1257.1	1638.5	1436.0	80.1
Jul 30	49.7	34.5	23.2	40.0	54	A	1143.2	1129.5	1552.8	1159.7	1163.6	1229.8	81.0
						E	1553.7	1308.7	1143.4	1121.7	1480.0	1321.5	86.8
Aug 27	33.2	32.7	21.5	37.4	49	A	671.5	1752.0	1202.0	1088.7	1362.3	1215.3	176.3
						E	1240.5	1207.1	932.9	1030.6	1025.4	1087.3	58.6
Aug 28	21.7	.	.	.	50	A	403.9	1067.8	750.6	744.6	872.9	768.0	108.2
						E	844.2	770.6	629.6	678.1	702.6	725.0	37.5
Sep 30	21.8	24.6	16.5	31.4	43	A	270.5	589.6	529.5	520.5	548.5	491.7	56.6
						E	488.7	563.4	346.0	577.6	567.4	508.6	43.6
Oct 01	14.8	27.8	15.7	33.2	42	A	370.0	749.9	651.8	694.3	709.4	635.1	68.1
						E	724.0	767.7	458.3	747.2	746.8	688.8	58.0
Oct 02	26.7	28.5	17.7	35.4	41	A	305.0	623.3	584.6	594.8	570.7	535.7	58.3
						E	625.3	636.7	411.4	629.5	687.1	598.0	48.0
Oct 29	25.8	16.7	3.9	21.7	39	A	15.7	60.8	47.4	57.1	44.7	45.1	7.9
						E	153.4	135.6	82.2	246.0	164.0	156.2	26.5
Oct 30	24.9	15.8	7.1	20.6	38	A	12.2	44.6	36.1	45.3	36.0	34.8	6.0
						E	201.9	134.1	149.1	258.8	236.3	196.0	24.1
		Chamber numbers :				Ambient	2	6	9	12	15		
						Elevated	1	4	8	11	13		

Table 5.3. Total daytime carbon uptake by the mixed community during 1988 for all days for which a complete dataset is available. The daytime period is defined as the period in which the light level exceeds 50 μmol m^{-2} s^{-1}. Shown are the total amount of light during this period, the mean, minimum and maximum temperature, the number of observations, the total daytime carbon uptake for the five ambient (A) and five elevated chambers (E), and the mean and standard error of the five chambers. The chamber numbers correlated with the ambient and elevated chambers of each block is given at the bottom of the table. Units for light are mol m^{-2} day^{-1}, units for carbon uptake are mmol m^{-2} day^{-1}.

	First day of carbon uptake	Day of maximum carbon uptake	Last day of carbon uptake	Maximum carbon uptake	Total carbon uptake 1988	Goodness of fit (R^2)
Scirpus						
Ambient	120.0*	179.0	361.1	755.6	1094	0.821
Elevated	120.0*	182.1	364.6	1330.5	1954	0.867
Spartina						
Ambient	108.0*	188.9	327.8	861.0	1134	0.950
Elevated	108.0*	178.3	361.7	1030.5	1567	0.935
Mixed						
Ambient	108.0*	200.6	329.9	1296.0	1727	0.892
Elevated	108.0*	190.3	341.0	1326.2	1906	0.882

Table 5.4. Results for daytime carbon uptake model described above for the three communities at ambient and elevated CO$_2$. The first day of carbon exchange is set to be equal to the first day at which green biomass is present. The values of the other parameters are found using a least squares curve fitting routine. The total carbon uptake is the cumulative value of the estimated daytime carbon uptake for all the days in the season (g C m^{-2} year^{-1}). Units are in Julian day, maximum carbon uptake is in mmol CO$_2$ m^{-2} day^{-1}.

	First day of carbon loss	Day of maximum carbon loss	Last day of carbon loss	Maximum carbon loss	Total carbon loss 1988	Goodness of fit (R^2)
Scirpus						
Ambient	92.0*	201.9	336.0*	192.6	282	
Elevated	92.0*	195.7	336.0*	148.9	218	
Spartina						
Ambient	92.0*	198.2	336.0*	254.5	368	0.718
Elevated	92.0*	191.1	336.0*	180.0	260	0.764
Mixed						
Ambient	92.0*	235.4	336.0*	270.0	396	0.526
Elevated	92.0*	213.4	336.0*	189.1	277	0.507

Table 5.5. Results for nighttime carbon loss model described above for the three communities at ambient and elevated CO$_2$. The first and last days of carbon loss are set to April 1st and December 1st. The values of the other parameters are found using a least squares curve fitting routine. The total carbon loss is the cumulative value of the estimated nighttime carbon loss for all the days in the season (g C m^{-2} year^{-1}). Units are in Julian day, maximum carbon loss is in mmol CO$_2$ m^{-2} day^{-1}.

Total carbon in aboveground biomass. Units in g m^{-2}.

	Senescent tissue			**Leaves**			**Stems**			**Total**
Treatm	% C	biom	tot C	% C	biom	tot C	% C	biom	tot C	carbon
Scirpus										
Amb	43.75	46.6	**20.39**				43.88	705.7	**309.7**	**330.1**
Elev	5.87	30.6	**14.04**				44.21	813.7	**359.7**	**373.7**
Spartina										
Amb	45.75	48.03	**21.97**	44.14	265.0	**116.9**	46.74	278.5	**130.1**	**269.0**
Elev	46.23	48.47	**22.40**	44.26	256.0	**113.3**	46.84	271.3	**127.1**	**262.8**
Distichlis										
Amb	43.49	15.67	**6.817**	45.12	50.58	**22.82**	47.36	113.4	**53.72**	**83.4**
Elev	44.28	25.81	**11.42**	45.35	74.96	**33.99**	47.25	167.9	**79.35**	**124.8**
Scirpus **(mixed)**										
Amb	39.04	13.19	**5.149**				39.04	27.62	**10.78**	**15.9**
Elev	43.72	28.62	**12.51**				43.72	125.3	**54.79**	**67.3**
Spartina **(mixed)**										
Amb	44.17	37.89	**16.73**	40.42	152.0	**61.44**	45.95	150.6	**69.22**	**147.4**
Elev	44.2	30.33	**13.40**	44.72	126.2	**56.45**	46.76	142.6	**66.68**	**136.5**
Mixed All species										
Ambient			**28.70**			**84.26**			**133.7**	**246.7**
Elevated			**37.33**			**90.44**			**200.8**	**328.6**

Table 5.6. Percent carbon, total biomass and total carbon in aboveground biomass of *Scirpus olneyi*, *Spartina patens* and *Distichlis spicata* in pure and mixed communities at peak standing biomass (end of July to beginning of September). The total carbon column contains the sum of the total carbon in senescent tissue, green leaves and green stems.

Percent Carbon

	Harvest 1			Harvest 2			Harvest 3			Harvest 4		
Scirpus olneyi in C3 community												
Green stems												
control	44.50	(0.12)	a	43.92	(0.04)	a	44.69	(0.08)	a	44.02	(0.18)	a
ambient	44.07	(0.19)	b	43.68	(0.11)	a	43.88	(0.17)	b	43.86	(0.20)	a
elevated	44.25	(0.06)	ab	43.83	(0.15)	a	44.21	(0.23)	ab	44.03	(0.09)	a
		p = 0.111			p = 0.338			p = 0.0209			p = 0.730	
Senescent tissue												
control	.	(.)		.	(.)		45.52	(0.61)	a	44.09	(0.34)	a
ambient	.	(.)		.	(.)		43.75	(0.60)	b	38.28	(1.96)	b
elevated	.	(.)		.	(.)		45.87	(0.52)	a	41.88	(0.38)	ab
								p = 0.0499			p = 0.0135	
Spartina in C4 community												
Green leaves												
control	44.40	(0.32)	a	44.94	(0.37)	a	44.54	(0.42)	a	43.89	(0.22)	a
ambient	43.55	(0.25)	b	44.22	(0.41)	a	44.14	(0.22)	a	42.98	(0.33)	b
elevated	43.94	(0.10)	ab	44.97	(0.31)	a	44.26	(0.31)	a	43.85	(0.17)	a
		p = 0.0812			p = 0.287			p = 0.679			p = 0.0406	
Green stems												
control	45.22	(0.32)	a	46.85	(0.18)	a	46.77	(0.25)	a	46.12	(0.17)	a
ambient	44.87	(0.26)	a	46.83	(0.15)	a	46.74	(0.22)	a	46.05	(0.16)	a
elevated	44.84	(0.26)	a	47.04	(0.13)	a	46.84	(0.21)	a	46.24	(0.11)	a
		p = 0.578			p = 0.601			p = 0.949			p = 0.730	
Senescent tissue												
control	.	(.)		47.04	(0.20)	a	47.31	(0.34)	a	44.47	(0.36)	a
ambient	.	(.)		43.38	(0.14)	b	45.75	(0.33)	b	43.34	(0.25)	b
elevated	.	(.)		44.16	(0.34)	b	46.23	(0.35)	b	44.45	(0.30)	a
					p = 0.0001			p = 0.0205			p = 0.0362	

Table 5.7. Percent carbon in aboveground biomass of *Scirpus olneyi*, *Spartina patens* and *Distichlis spicata* in pure and mixed communities. Mean and standard error of five chambers, means with the same letter are not significantly different at the 0.05 level.

	Harvest 1			Harvest 2			Harvest 3		
<u>Scirpus olneyi in Mixed community</u>									
Green stems									
control	44.04	(0.26)	a	43.43	(0.93)	a	44.26	(0.50)	a
ambient	43.69	(0.28)	a	39.04	(1.44)	b	42.50	(0.54)	b
elevated	43.78	(0.22)	a	43.72	(0.59)	a	43.64	(0.32)	ab
		p = 0.610			p = 0.0132			p = 0.066	
Senescent tissue									
control	.	(.)		.	(.)		42.53	(0.92)	a
ambient	.	(.)		.	(.)		33.59	(0.28)	b
elevated	.	(.)		.	(.)		39.36	(1.36)	a
								p = 0.0008	
<u>Spartina in Mixed community</u>									
Green leaves									
control	44.65	(0.26)	a	44.81	(0.49)	a	45.37	(0.14)	a
ambient	44.07	(0.29)	a	40.42	(4.16)	a	44.19	(0.28)	b
elevated	44.57	(0.23)	a	44.72	(0.54)	a	45.19	(0.07)	ab
		p = 0.278			p = 0.467			p = 0.0078	
Green stems									
control	45.42	(0.17)	a	46.92	(0.14)	a	46.60	(0.19)	a
ambient	44.67	(0.42)	a	45.95	(0.60)	a	46.54	(0.10)	a
elevated	45.19	(0.16)	a	46.76	(0.24)	a	46.41	(0.15)	a
		p = 0.247			p = 0.266			p = 0.655	
Senescent tissue									
control	.	(.)		45.60	(0.59)	a	44.68	(0.35)	a
ambient	.	(.)		44.17	(0.75)	a	43.76	(0.23)	b
elevated	.	(.)		44.20	(1.14)	a	44.14	(0.13)	ab
					p = 0.443			p = 0.0725	
<u>Distichlis in Mixed community</u>									
Green leaves									
control	46.05	(0.47)	a	45.29	(0.51)	a	45.65	(0.29)	a
ambient	45.89	(0.15)	a	45.12	(0.63)	a	45.49	(0.16)	a
elevated	45.79	(0.16)	a	45.35	(0.44)	a	45.85	(0.29)	a
		p = 0.843			p = 0.951			p = 0.627	
Green stems									
control	46.09	(0.30)	a	47.35	(0.43)	a	47.16	(0.17)	a
ambient	46.20	(0.25)	a	47.36	(0.26)	a	47.00	(0.23)	a
elevated	46.04	(0.24)	a	47.25	(0.35)	a	47.25	(0.26)	a
		p = 0.913			p = 0.968			p = 0.735	
Senescent tissue									
control	.	(.)		44.92	(1.07)	a	45.19	(0.42)	a
ambient	.	(.)		43.49	(0.38)	a	45.16	(0.14)	a
elevated	.	(.)		44.28	(0.34)	a	44.81	(0.64)	a
					p = 0.368			p = 0.795	

	Rhizomes	Roots
Scirpus (C3)		
control	45.72 (0.58) a	45.52 (0.24) a
ambient	45.10 (0.66) a	45.39 (0.32) a
elevated	44.92 (0.61) a	45.77 (0.29) a
	p = 0.654	p = 0.638
Spartina (C4)		
control	46.24 (0.09) a	47.56 (0.16) a
ambient	46.11 (0.11) a	47.31 (0.20) a
elevated	45.98 (0.10) a	47.21 (0.17) a
	p = 0.194	p = 0.346
Mixed (C3+C4) (C4 rhizomes)		
control	46.46 (0.18) a	45.75 (0.28) a
ambient	46.19 (0.18) a	45.64 (0.23) a
elevated	46.40 (0.08) a	46.24 (0.65) a
	p = 0.440	p = 0.575

Table 5.8. Percent carbon in belowground biomass of *Scirpus olneyi*, *Spartina patens* and *Distichlis spicata* in regrowth cores of pure and mixed communities. Values shown are mean and standard error. Means with the same letter are not significantly different at the 0.05 level.

Total carbon in belowground biomass (regrowth cores). Units in g m^{-2}.

	Roots			C4 rhizomes			C3 rhizomes			Total
Treatm	% C	biom	tot C	% C	biom	tot C	% C	biom	tot C	carbon
Scirpus										
Amb	45.39	181.7	**82.47**				45.10	210.1	**94.76**	**177.2**
Elev	45.77	296.7	**135.8**				44.92	183.5	**82.43**	**218.2**
Spartina										
Amb	47.31	120.0	**56.77**	46.11	97.54	**44.98**				**101.8**
Elev	47.21	153.4	**72.42**	45.98	121.5	**55.87**				**128.3**
Mixed										
Amb	45.64	178.1	**81.28**	46.19	120.8	**55.80**	47.43	2.23	**1.06**	**138.1**
Elev	46.24	223.3	**103.3**	46.40	121.1	**56.19**	44.80	60.75	**27.22**	**186.7**

Table 5.9. Percent carbon, total biomass and total carbon in roots and rhizomes of regrowth cores in the *Scirpus*, *Spartina* and Mixed community.

	Daytime carbon uptake	Nighttime carbon loss	Net carbon gain	Carbon in aboveground biomass
Scirpus				
Ambient	1094	282	812	330
Elevated	1954	218	1736	373
E - A	**860**	**-64**	**924**	**44**
Spartina				
Ambient	1134	368	766	269
Elevated	1567	260	1307	263
E - A	**433**	**-108**	**541**	**-6**
Mixed				
Ambient	1727	396	1331	247
Elevated	1906	277	1629	329
E - A	**179**	**-119**	**298**	**82**

Table 5.10. Carbon uptake and loss during 1988 and total carbon present in aboveground tissues at peak standing biomass of the *Scirpus*, *Spartina* and Mixed community. Shown are estimated values for ambient and elevated chambers and the difference between elevated and ambient chambers. The units are gram carbon per meter square.

Chapter 6. Evapo–transpiration and water potential.

Evapo–transpiration

Reduction of transpiration of plants is the most commonly observed effect of elevated CO_2, occurring both in C_3 and C_4 plants. The carbon uptake by C_4 species usually does not increase very much at elevated CO_2 when growth conditions are optimal, but may show a substantial increase if the carbon uptake is limited by drought or salt stress which can be alleviated by elevated CO_2.

Methods

Measurements of canopy evapo-transpiration were made on closed top chambers, in a way identical to the measurement of canopy CO_2 exchange (chapter 5). The water vapor concentration of the air entering and exiting the chamber was measured using dew point hygrometers, and the difference in dew point values was converted to evapo-transpiration in mmol H_2O m^{-2} s^{-1}. No measurements could be made in the morning hours because overnight dew formation in the chambers and gas circuit obscured the measurements. Good readings were usually obtained from 12:00 to 17:00 h.

Water use efficiency is calculated as the number of moles of carbon dioxide absorbed by the canopy per mol of water lost to evapo-transpiration. Mean carbon uptake, mean water loss, and water use efficiency were calculated for the period 14:00 - 16:00 h for each day for which data were available.

Results

The evapo-transpiration and canopy water use efficiency during the course of one day of the 1988 season is shown in figure 6.1 for each of the three communities, in relation to canopy CO_2 exchange, light and temperature.

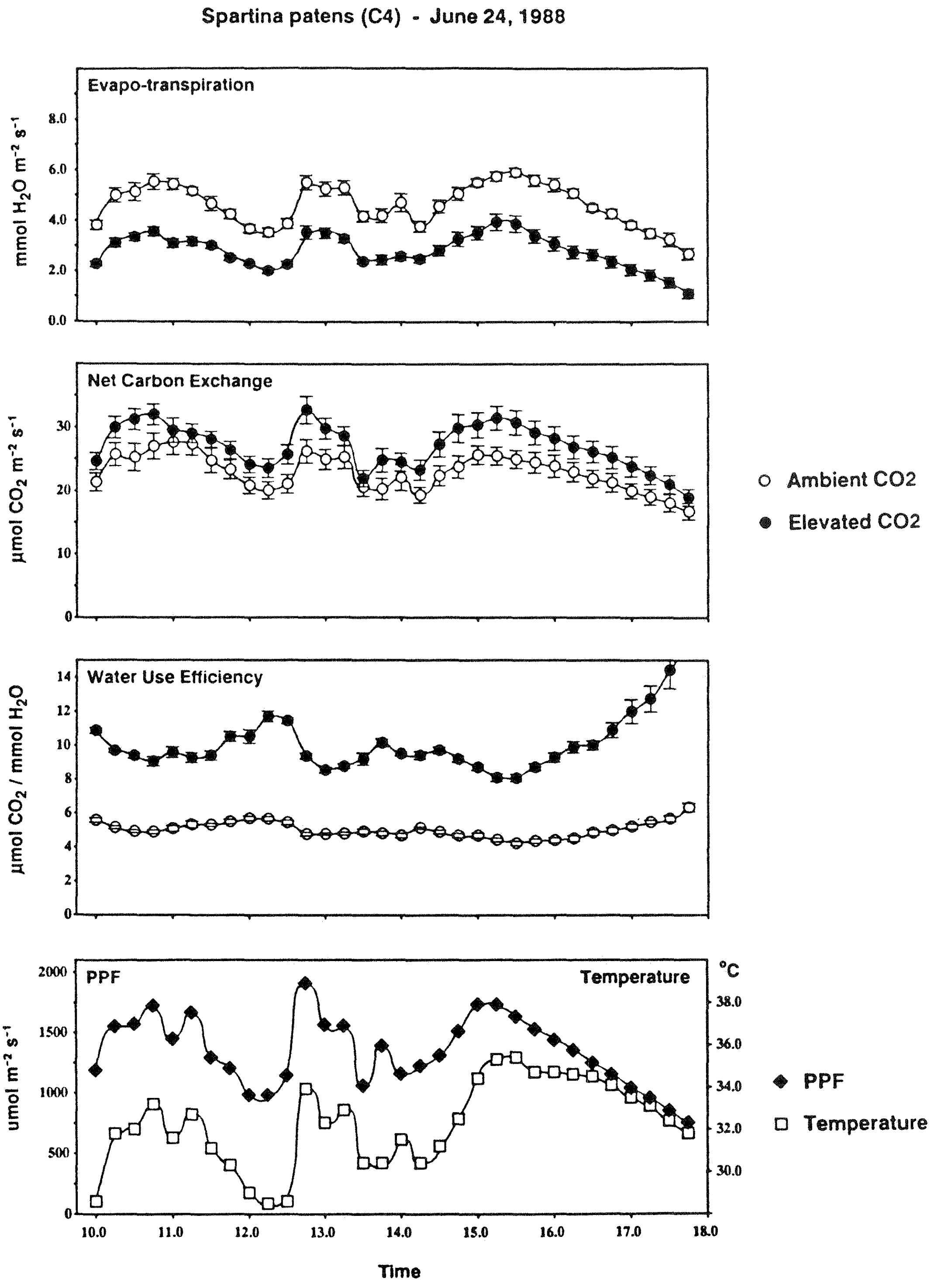


Figure 6.1. Evapo-transpiration, canopy CO$_2$ exchange, water use efficiency, light and temperature for one day for each of the three communities. Values shown are mean and standard error for five chambers for a 15 minute period.

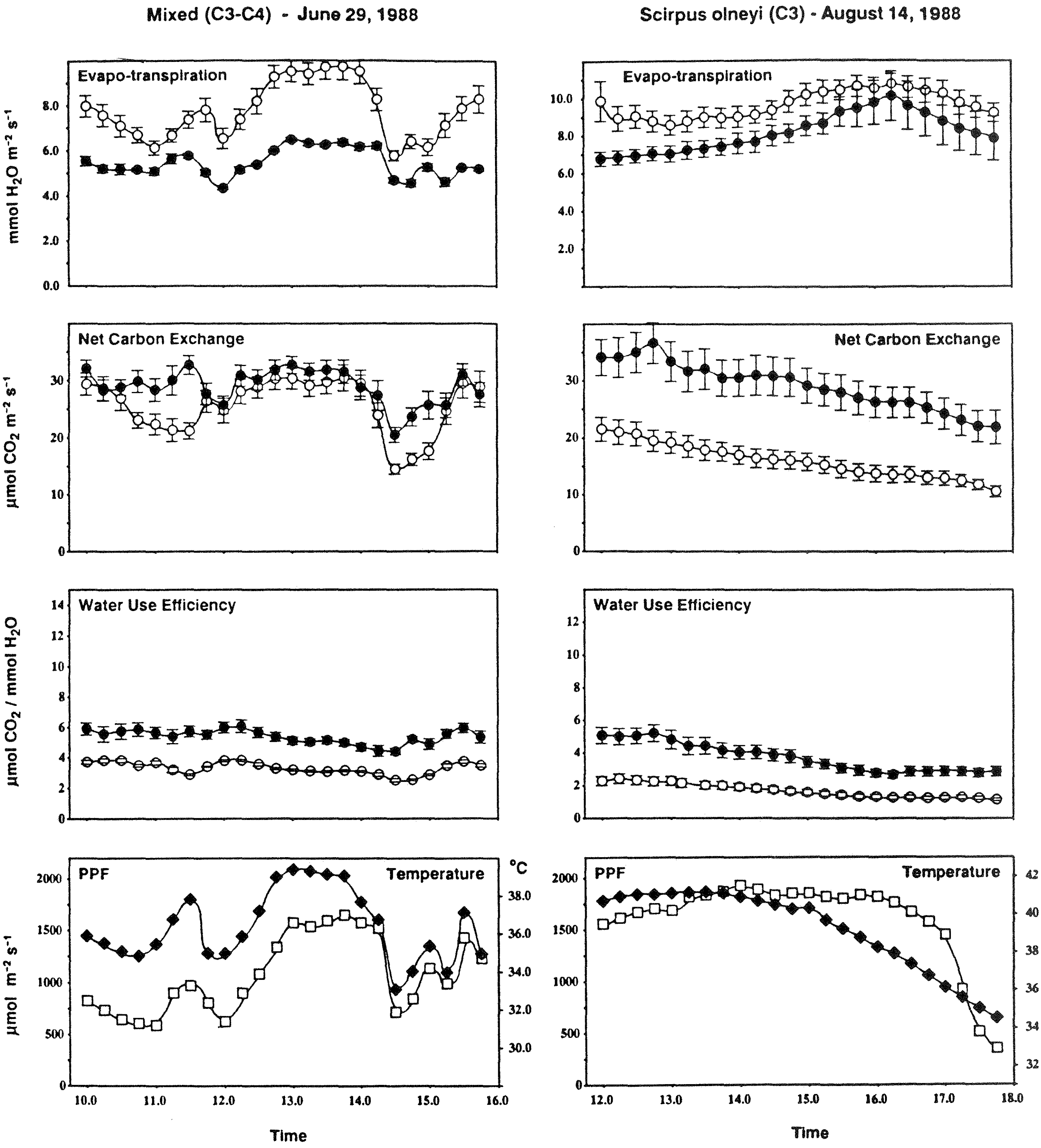

Mixed (C3-C4) - June 29, 1988
Scirpus olneyi (C3) - August 14, 1988
Evapo-transpiration
mmol H_2O m^{-2} s^{-1}
0.0
2.0
4.0
6.0
8.0
10.0
Net Carbon Exchange
µmol CO_2 m^{-2} s^{-1}
0
10
20
30
Water Use Efficiency
µmol CO_2 / mmol H_2O
0
2
4
6
8
10
12
14
PPF
Temperature
°C
µmol m^{-2} s^{-1}
0
500
1000
1500
2000
30.0
32.0
34.0
36.0
38.0
32
34
36
38
40
42
10.0
11.0
12.0
13.0
14.0
15.0
16.0
17.0
18.0
Time

Figure 6.2 summarizes the evapo-transpiration data throughout the 1988 season. Each data point in this figure is the mean value for the time period 14:00 to 16:00 h for five chambers for one day. The percent decrease in transpiration due to elevated CO_2 is shown on the right hand side of the graph.

Evapo-transpiration per meter square ground area was highest in the *Scirpus* and lowest in the *Spartina* community. Elevated CO_2 reduced the evapo-transpiration in all three communities. The average decrease in transpiration for the period June, July and August was 25% for *Scirpus*, 29% for *Spartina* and 32% for the mixed community.

Water use efficiency was calculated for the same time periods and the results are presented in figure 6.3. In ambient CO_2 the water use efficiency was lowest in the *Scirpus* and highest in the *Spartina* community. This is in agreement with the theory that C_4 plants are more efficient with water than C_3 plants. In all three communities elevated CO_2 increased the water use efficiency, but the increase was largest in the *Scirpus* community as a result of the large enhancement in carbon uptake. As a consequence, the levels of water use efficiency at elevated CO_2 is approximately the same for all three communities.

A summary of the effect of elevated CO_2 on carbon uptake, evapo-transpiration and water use efficiency is given in figure 6.4. The data points are means for the period June, July and August 1988. The relative increase as an effect of elevated CO_2 is shown in figure 6.5.

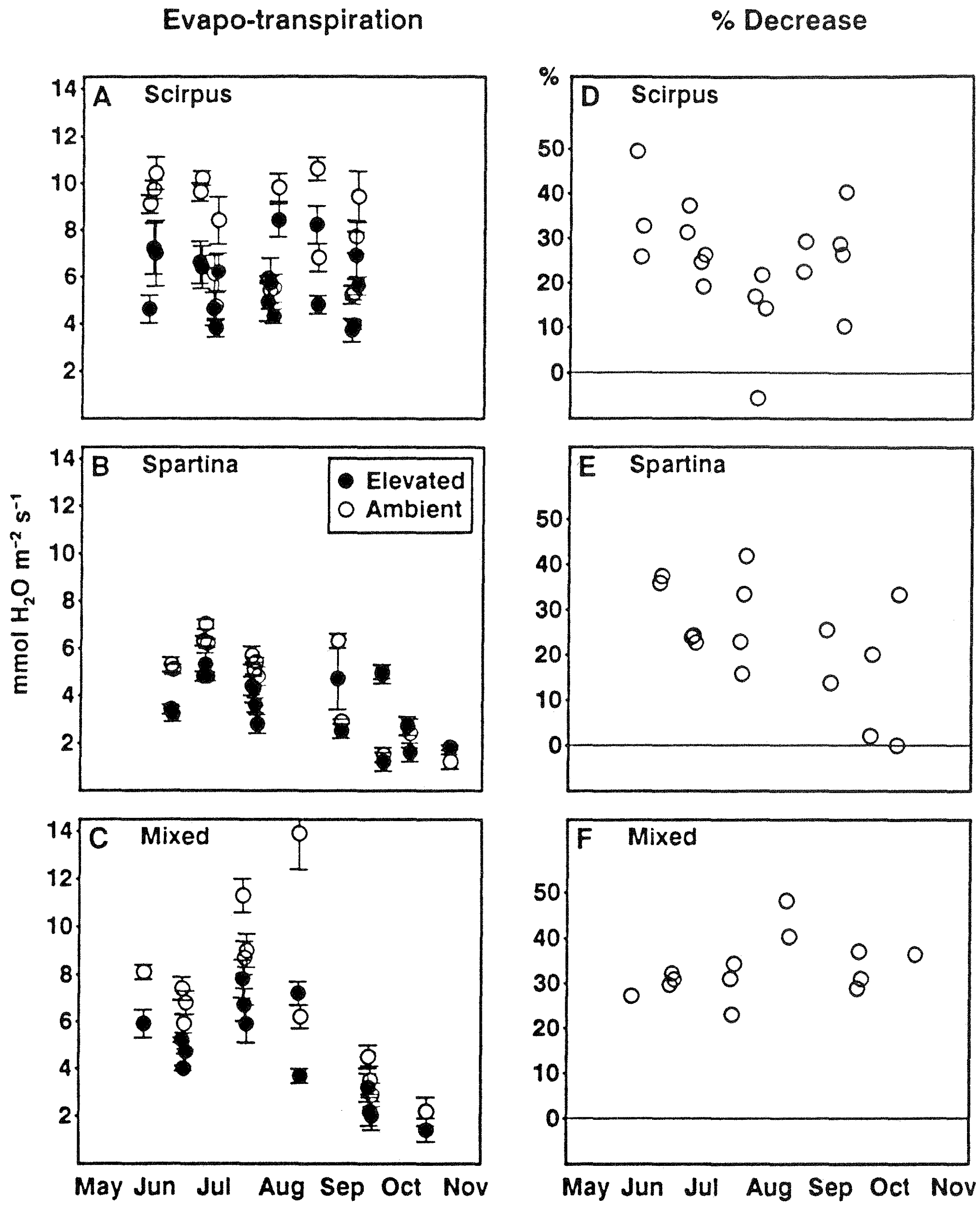


Figure 6.2. Mean evapo-transpiration for the period 14:00 to 16:00 h (A,B and C) and percent decrease in evapo-transpiration (D,E and F) for the three communities during the 1988 season. Open circles represent the mean of five ambient chambers, the closed circles stand for the elevated chambers.

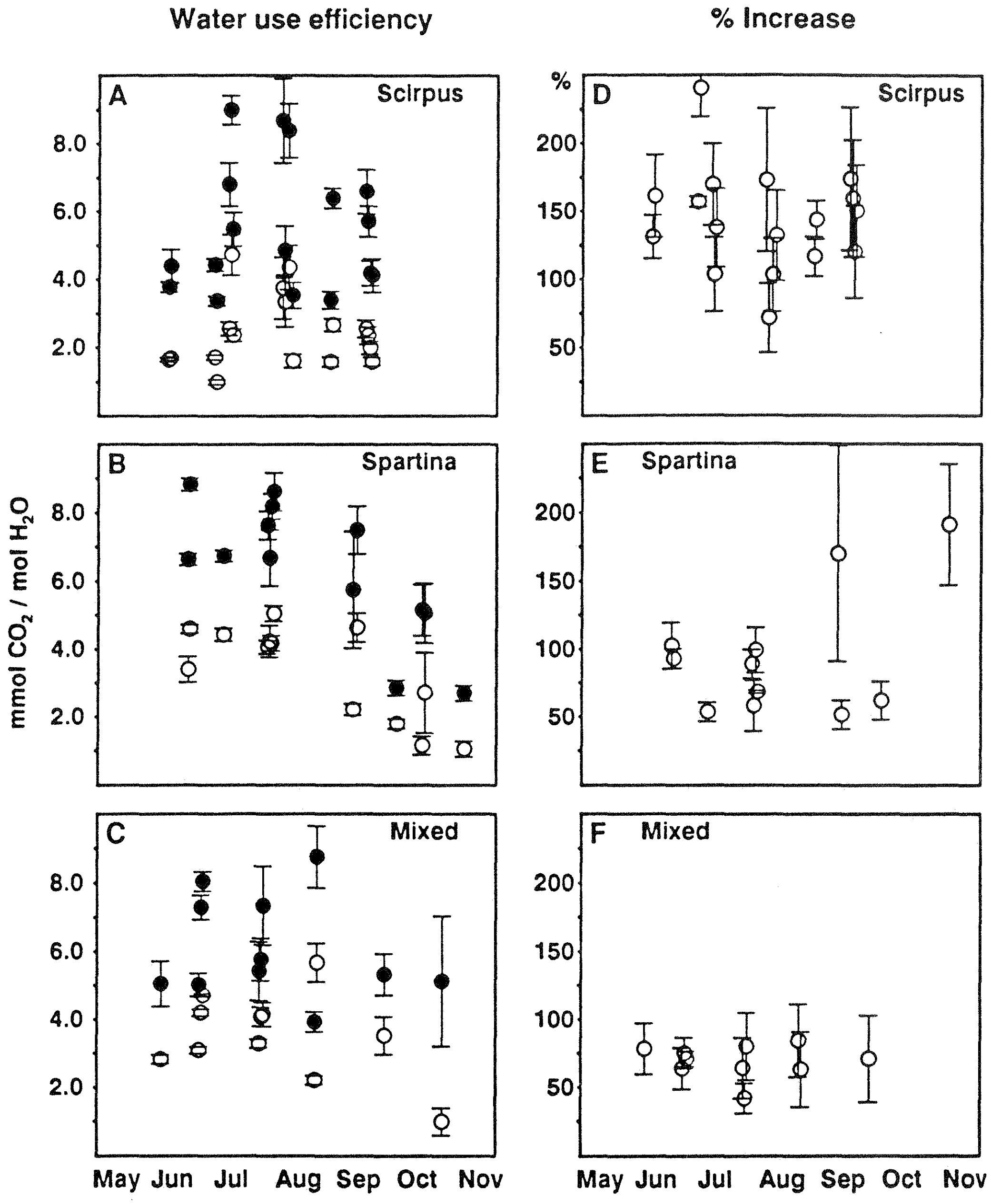


Figure 6.3. Water use efficiency (A,B and C) and percent increase in water use efficiency (D,E and F) for the three communities during the 1988 season. Water use efficiency was calculated using evapo-transpiration and net carbon uptake values for the period 14:00 to 16:00 h. Open circles represent the mean of five ambient chambers, the closed circles stand for the elevated chambers.

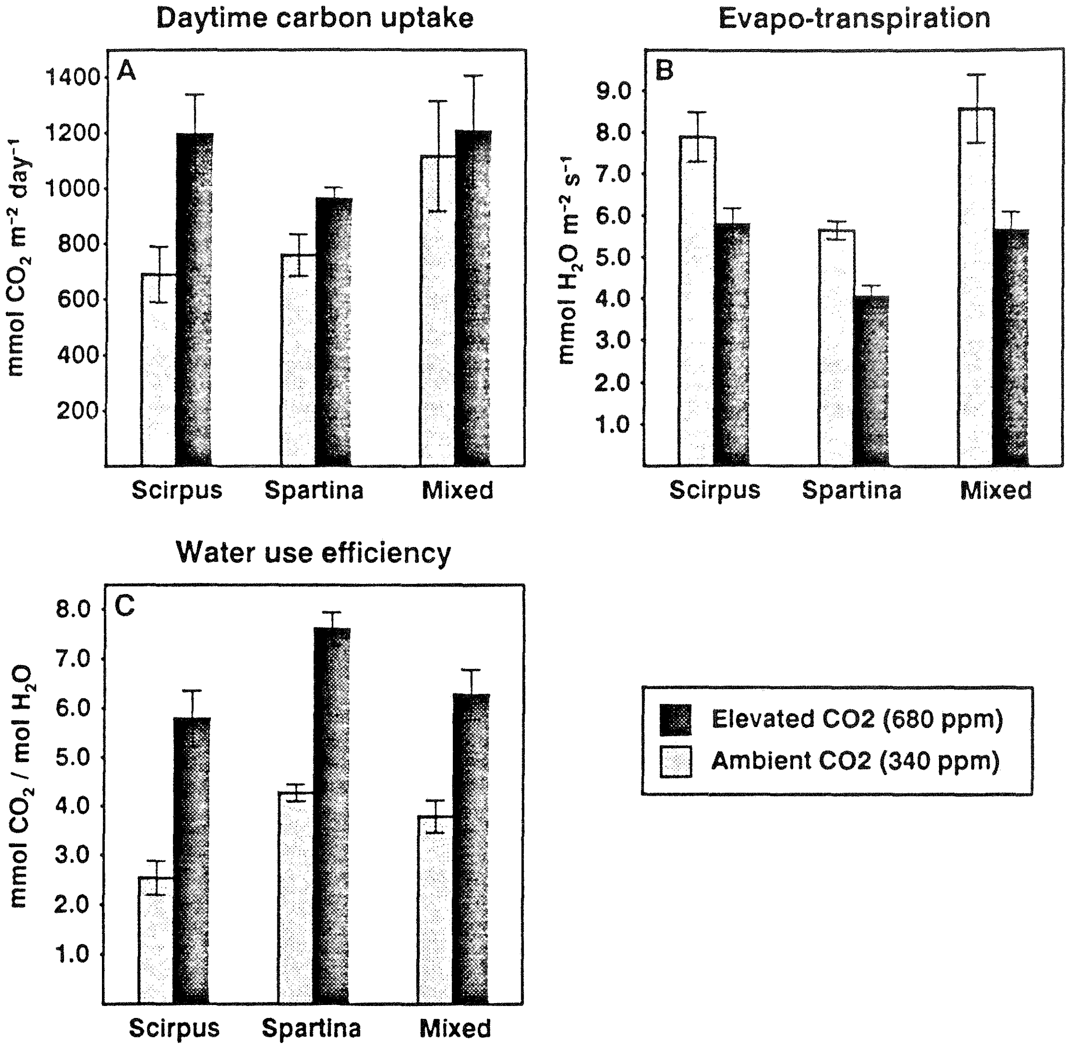


Figure 6.4. Daytime carbon uptake (A), Evapo-transpiration (B) and water use efficiency (C) the three communities. Bars represent means and standard error of all measurements during June, July and August of 1988. Water use efficiency was calculated using evapo-transpiration and net carbon uptake values for the period 14:00 to 16:00 h.

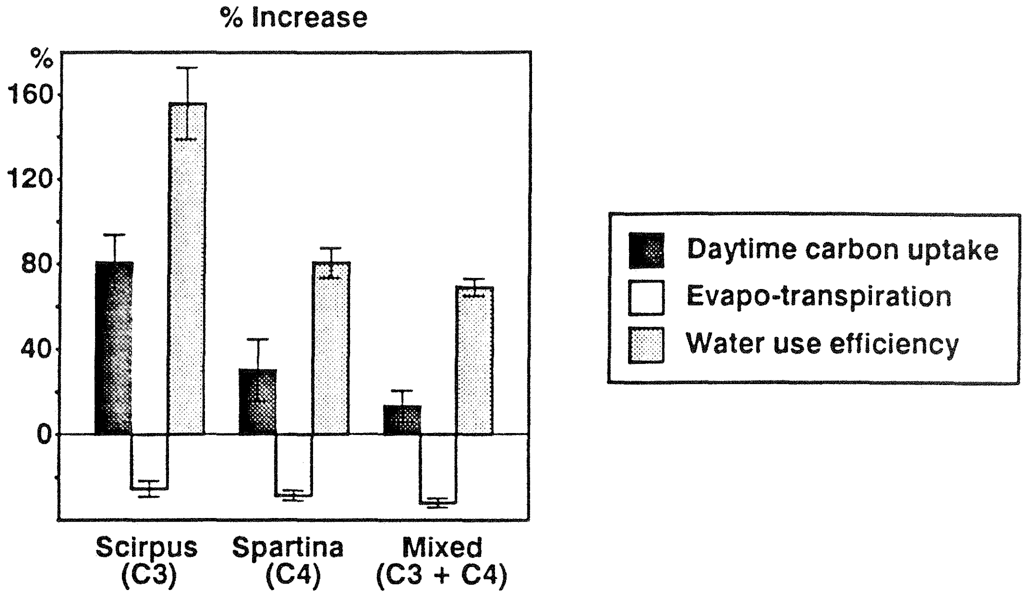


Figure 6.5. The effect of elevated CO_2 (expressed as percent increase) on daytime carbon uptake, evapo-transpiration and water use efficiency for the three communities during June, July and August of the 1988 season.

Water potential.

The water potential of plants is the tension on the xylem water column created by water loss through transpiration which in turn is the driving force for water uptake by the roots. The water potential is most negative when the rate of water loss is greatest or when the water uptake is restricted by a low soil water potential which can be caused by drought or a high salinity. Reduction of water loss by evapotranspiration as a result of elevated CO_2 is expected to improve the water balance in the plant. This is reflected in an increased (less negative) water potential of plants growing in elevated CO_2 compared to plants grown in normal ambient CO_2.

Methods

The water potential of *Scirpus* and *Spartina* shoots from ambient and elevated chambers and from control sites was measured using a Scholander pressure bomb. Measurements of midday water potential were made weekly during the months June, July and August, while pre-dawn measurements were made every two weeks.

Soil water salinity was measured at regular intervals in wells which were established in the chambers and control sites in 1986. For each community and treatment there are two sets of wells, each set consisting of four PVC pipes extending 15, 30, 50 and 100 cm into the marsh. Water was extracted from these wells using a hand pump, and the salinity was measured using a refractometer.

Results

The water potential at midday when the transpiration rate is highest is shown in figure 6.6 for shoots of *Scirpus* and *Spartina* from the pure communities. Elevated CO_2 increased the water potential of both *Scirpus* and *Spartina*, the relative increase being largest in *Scirpus*.

During the night stomatal closure prevents transpiration and the water status of the plants is able to recover. At the end of the dark period the water potential of

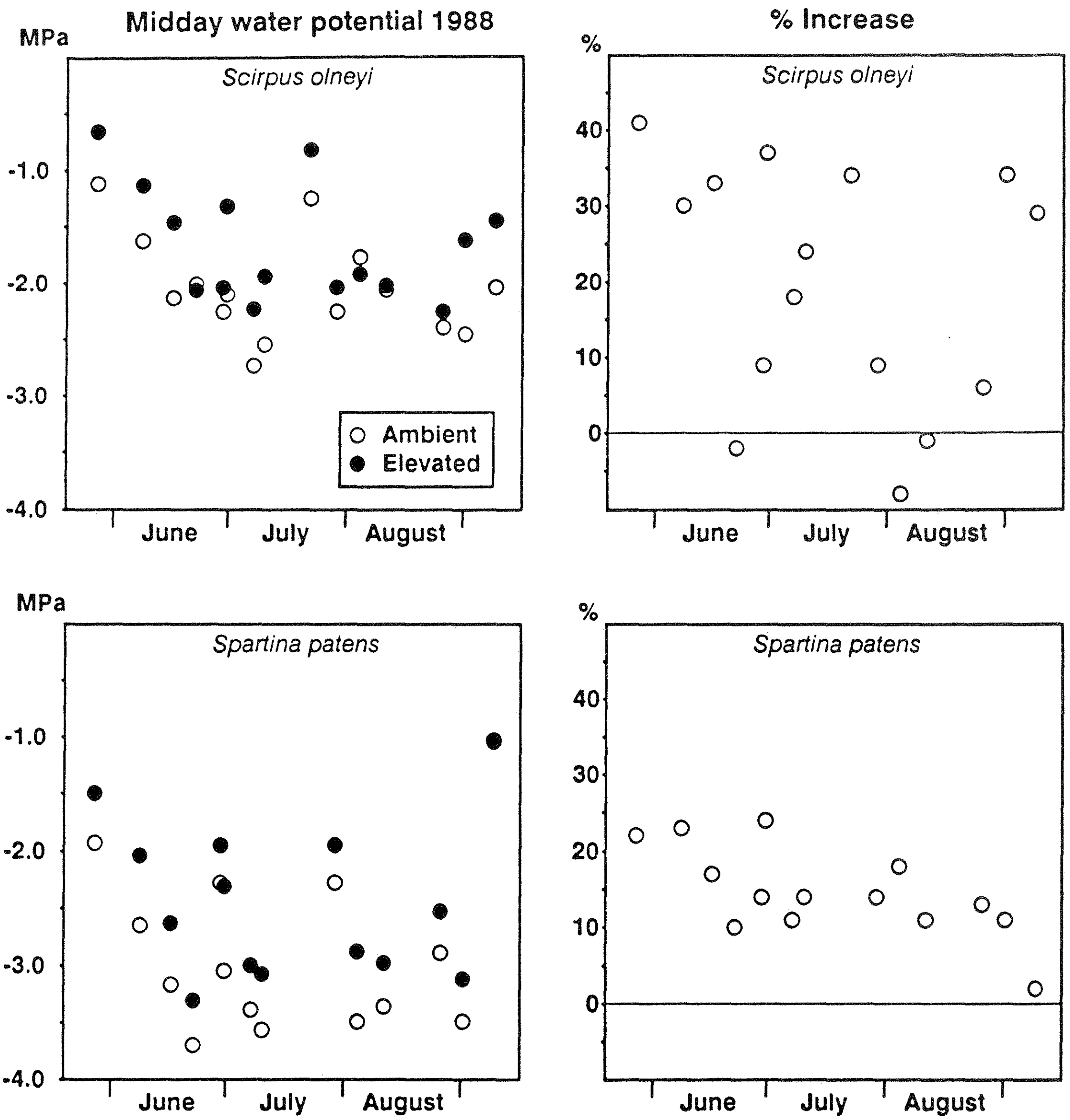


Figure 6.6. Midday water potential of *Scirpus olneyi* (A) and *Spartina patens* (B). The effect of elevated CO_2 (as percent increase) on the water potential is shown in C and D.

the plant will be close to the water potential of the water source of the plant. The results of pre-dawn water potential measurements are shown in figure 6.7. A comparison between the pre-dawn water potential and the soil water potential at different depth is made in figure 6.8. The data points presented in this graph are the mean values for the period June - August. The soil water salinity was higher in the *Spartina* than in the *Scirpus* community, and the salinity decreased with depth. The pre-dawn water potential of *Spartina* was similar to the soil water potential at 15, 30 or 50 cm, while the pre-dawn water potential of *Scirpus* was much less negative, and comparable to the soil water salinity at 100 cm. This suggest that *Scirpus* is able to tap the relatively fresh water at greater depth, while the water source of *Spartina* is limited to the more saline upper layer of the marsh.

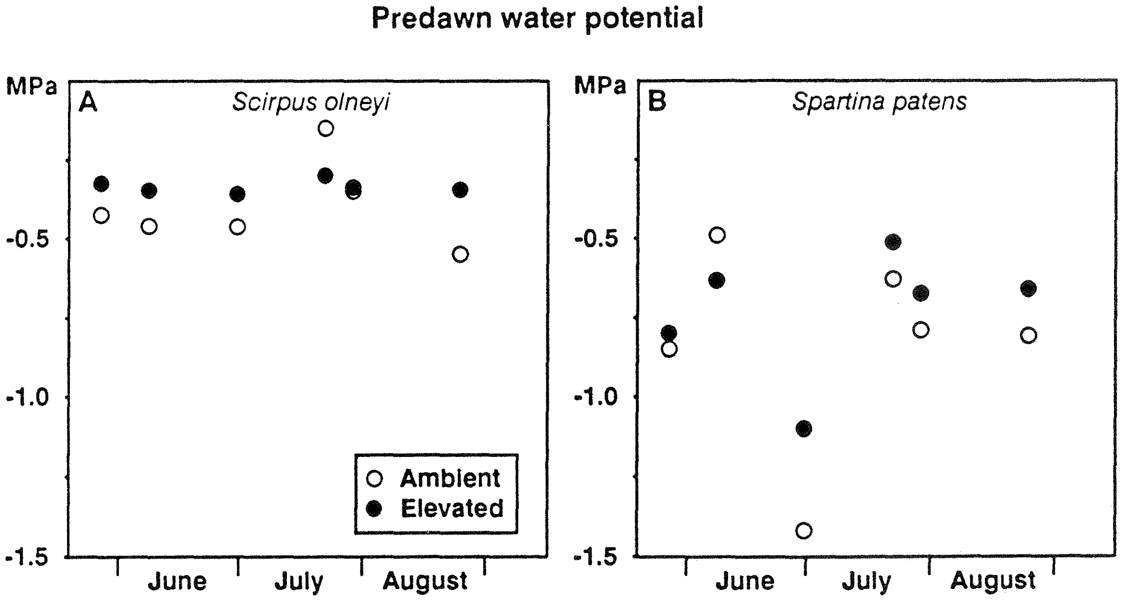


Figure 6.7. Pre-dawn water potential of *Scirpus olneyi* (A) and *Spartina patens* (B). Symbols represent mean values of all measurements for one day.

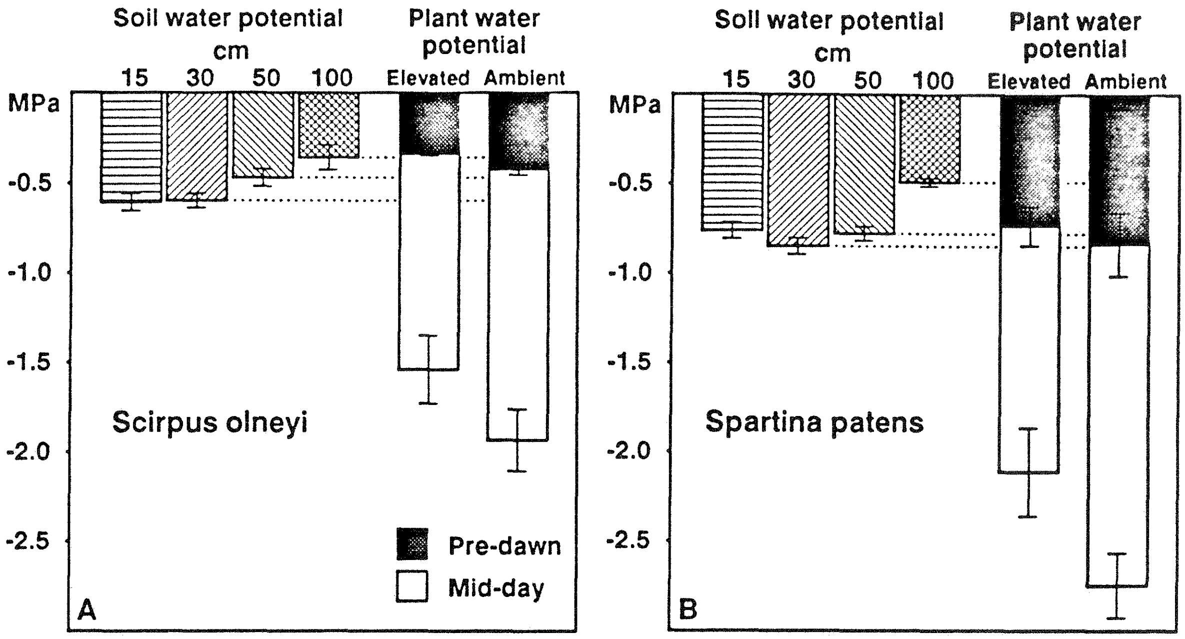


Figure 6.8. Soil water potential at four different depths in the marsh and the pre-dawn and mid-day water potential of elevated and ambient plants of *Scirpus olneyi* (A) and *Spartina patens* (B). The dotted lines show the correlation between pre-dawn water potential and soil water potential at the different depths.

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