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Nitrogen and carbon dynamics in C₃ and C₄ estuarine marsh plants grown under elevated CO₂ in situ

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Summary. Carbon dioxide concentrations were elevated in three estuarine communities for an entire growing season. Open top chambers were used to raise CO₂ concentrations ca. 336 ppm above ambient in monospecific communities of *Scirpus olneyi* (C₃) and *Spartina patens* (C₄), and a mixed community of *S. olneyi*, *S. patens* and *Distichlis spicata* (C₄). Nitrogen and carbon concentration (% wt) of above-ground tissue was followed throughout growth and senescence. Green shoot %N was reduced and %C was unchanged under elevated CO₂ in *S. olneyi*. This resulted in a 20%–40% increase in tissue C/N ratio. There was no effect of CO₂ on either C₄ species. Maximum aboveground N (g/m²) was unchanged in *S. olneyi*, indicating that increased productivity under elevated CO₂ was dependent on reallocation of stored N. There was no change in the N recovery efficiency of *S. olneyi* in pure stand and a decrease in the mixed community. Litter C/N ratio was not affected by elevated CO₂ suggesting that decomposition and N mineralization rates will also remain unchanged. Continued growth responses to elevated CO₂ could, however, be limited by the ability of *S. olneyi* to increase the total above-ground N pool.

Key words: Carbon dioxide – Nitrogen – *Spartina* – *Scirpus* – Wetlands

The steadily increasing concentration of CO₂ in the earth's atmosphere is expected to have a number of important effects on terrestrial vegetation. Crop plants as well as wild species show increased photosynthesis, water use efficiency, and growth under elevated CO₂ (Kimball 1983; Oechel and Strain 1985) although not all species respond to the same degree. In particular, plants with the C₃ photosynthetic pathway typically respond more to increases in CO₂ concentration than do plants with the C₄ photosynthetic pathway (Acock and Allen 1985). This differential sensitivity can lead to changes in competitive ability (Zangerl and Bazzaz 1984) and potentially to changes in community composition (Bazzaz et al. 1985).

A less well understood effect of elevated CO₂ is the change in elemental composition of plant tissues, particularly the carbon and nitrogen content. Changes in the C/N

ratio of natural vegetation could have a profound impact on ecosystem functioning, affecting nutrient use efficiency (Vitousek 1982; Field and Mooney 1986), herbivory (Scriber 1984), and nutrient cycling (Melillo et al. 1984). Limited data suggest that C/N ratios of C₃ species could increase substantially with increasing atmospheric CO₂ concentrations. In annual species, increased photosynthetic rates under high CO₂ often lead to an accumulation of carbohydrates in leaves and an increase in specific leaf weight (Acock and Allen 1985). This may occur to a much lesser degree in species with high growth rates or strong carbon sinks (Cure et al. 1987). Leaf nitrogen, protein, and ribulose biphosphate carboxylase levels have been observed to decline in C₃ crop plants grown under high CO₂ (Wong 1979; Vu et al. 1983; von Caemmerer and Farquhar 1984).

The diversity of individual species responses to elevated CO₂ and the important role of environmental factors in modifying these responses has made it difficult to extrapolate from these few studies on agricultural plants to unmanaged plant communities. In one of the first studies of natural populations, we have exposed intact C₃ and C₄ marsh canopies to a doubling in atmospheric CO₂ concentration for an entire growing season. Our results show that C/N ratios increase in the C₃ species only, and that greater productivity under elevated CO₂ may come at the expense of lower shoot N.

Materials and methods

Three plant communities on a brackish marsh of the Rhode River, a sub-estuary of the Chesapeake Bay, were exposed to elevated CO₂ concentrations for an entire growing season. The study site and experimental design have been described in detail previously (Curtis et al. 1989). One community was dominated by the C₄ grass *Spartina patens*, and another by the C₃ sedge *Scirpus olneyi*. The third was a mixture of *S. patens*, *S. olneyi*, and *Distichlis spicata*, a C₄ grass.

Fifteen permanent circular plots, 0.8 m in diameter, were established along transect lines in each community. Treatments were assigned to plots according to a randomized block design, with three treatments per block and five blocks per community. Within each community five plots had exposure chambers (described below) with CO₂ concentrations ca. 336 ppm above ambient levels (Elevated treatment), five plots had chambers receiving no additional CO₂ (Ambient treatment) and five plots had no chambers but

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were treated identically to chambered plots (Control treatment).

Open top chambers were used to elevate CO₂ within a plot (Drake et al. 1987). Chambers were 0.8 m in diameter, 1.2 m in height, and were covered with 300 µm polyester film. Ambient air was introduced into the chamber by a high capacity blower and circulated within the chamber by a second blower. CO₂ was elevated within a chamber by continuously injecting 100% CO₂ into the input blower where it was mixed with ambient air before entering the chamber. Seasonal mean CO₂ concentrations (sunrise to sunset) were 350 ± 22 µl l⁻¹ inside Ambient plots (mean ± s.d.) and 686 ± 30 µl l⁻¹ inside Elevated plots. Treatments were begun April 23, 1987 and terminated November 15, 1987.

Serial harvests of green tissue were made in each plot beginning in late April and senescent tissue was collected in late December. Shoots were harvested randomly with respect to age and position in the plot. Reproductive tissue (seeds and bracts) in the *Scirpus* community was harvested in August after seeds had begun to be shed. Harvested material was dried at 60°C and ground to pass through a 1.0 mm screen with a Wiley mill. Nitrogen (N) and carbon (C) were analysed with a Carbon-Hydrogen-Nitrogen analyser (Control Equipment Corp., Lowell MA) at the University of Maryland, Horn Point Laboratory. Nitrogen and carbon content were calculated on a % by weight basis. Similar results were obtained when N was expressed on an area basis since there were no significant CO₂ effects on specific leaf weight (Curtis et al. 1989).

Aboveground biomass was estimated using nondestructive censuses of shoot number and height (Curtis et al. 1989). Litter production was calculated as the cumulative total of senescent tissue produced during the season. Canopy N was calculated as the product of aboveground biomass and whole shoot %N at a given census, with maximum aboveground N (M_N) present at peak standing biomass. Litter N (L_N) was calculated from the product of total litter biomass and %N of fully senescent shoots. The percentage of maximum aboveground N which was translocated belowground, out of senescing tissue, was expressed as the recovery efficiency (R) (Melillo et al. 1984), where:

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

Results from the serial harvest were analysed for overall treatment effects using repeated measures analysis of variance (SAS Institute 1985). Single degree of freedom contrasts (Elevated vs Ambient, Ambient vs Control) within a harvest were made by univariate analysis of variance. All percentages and ratios were arcsin transformed before analysis.

Results

Scirpus shoots grown under elevated CO₂ had significantly lower %N than those exposed to normal ambient CO₂ concentrations in the pure and mixed communities (Table 1, Fig. 1A and 1B). The effect of CO₂ was not constant over the growing season, with significant differences between Elevated and Ambient treatments first becoming apparent in June. CO₂ effects were again nonsignificant in November in the mixed community. There were no significant differences between Ambient and Control treatments at any time

Table 1. Results of repeated measures analysis of variance testing for treatment effects on leaf nitrogen content in three salt marsh species

Species – Community	<i>F</i>	<i>P</i> <
<i>Scirpus</i> – Pure	4.82	0.029
<i>Scirpus</i> – Mixed	19.53	0.0004
<i>Spartina</i> – Pure	3.62	0.076
<i>Spartina</i> – Mixed	0.62	0.556
<i>Distichlis</i> – Mixed	1.07	0.372

(data not shown). Percent carbon varied only slightly throughout the season and there were no significant effects on *Scirpus* in either community (Fig. 1).

There were no significant CO₂ effects on leaf %N in either C₄ species in the pure or mixed communities (Table 1). The seasonal progression of leaf %N in *Spartina* that is shown in Fig. 1C is representative of both C₄ species from either community. Tissue %N was high early in the season but fell sharply in late May to a fairly constant level of about 0.8%. In this instance, a small but significant difference in tissue %N was observed in August. This was most likely due to unusually high %N in the Ambient treatment rather than lower %N under elevated CO₂ since Controls were also lower than Ambients at this harvest. No differences were seen in the other C₄ samples. Tissue %C was similar to that in *Scirpus* and was unaffected by CO₂ (Fig. 1C).

The decrease in tissue %N in *Scirpus* under elevated CO₂ caused a significant increase in C/N ratios in both communities (Fig. 2). *Scirpus* in pure stand showed a 20–30% increase in shoot C/N between August and November. In the mixed community the effect varied between a 20% and 40% increase in C/N. There was no significant effect of CO₂ on senescent tissue, however. Dead *Scirpus* shoots had higher C/N ratios than living shoots but there were no significant differences between Elevated and Ambient treatments (Fig. 2).

Although tissue %N was reduced in *Scirpus* from the pure community, increased growth under elevated CO₂ offset this reduction, resulting in no net effect on total canopy N (Fig. 3). Lower canopy N in mid-June was due to slightly lower initial canopy biomass in Elevated sites. Maximum aboveground N was not affected by elevated CO₂ in *Scirpus* from either community or in *Spartina* (Fig. 4). Total litter N, while unaffected by CO₂ in *Scirpus* in pure stand, increased significantly ($P < 0.05$) in *Scirpus* from the mixed community. *Spartina* had less than half the maximum aboveground N of *Scirpus* in pure stand but left almost identical amounts of N in litter. This difference between *Scirpus* and *Spartina* is reflected in their two fold difference in N recovery efficiency (Fig. 4, inset). Under ambient CO₂, *Scirpus* in the mixed community had an N recovery efficiency intermediate between *Scirpus* and *Spartina* in pure stand. This was reduced under elevated CO₂, falling to below that found in *Spartina*.

There was no difference in %C or %N of seeds from *Scirpus* in pure stand between Elevated and Ambient treatments (Table 2). The enveloping bracts, however, behaved similarly to other shoot tissue, with significantly less %N under elevated CO₂. There was a chamber effect in seed %C and %N, with Controls having higher %C and lower %N than Ambients.

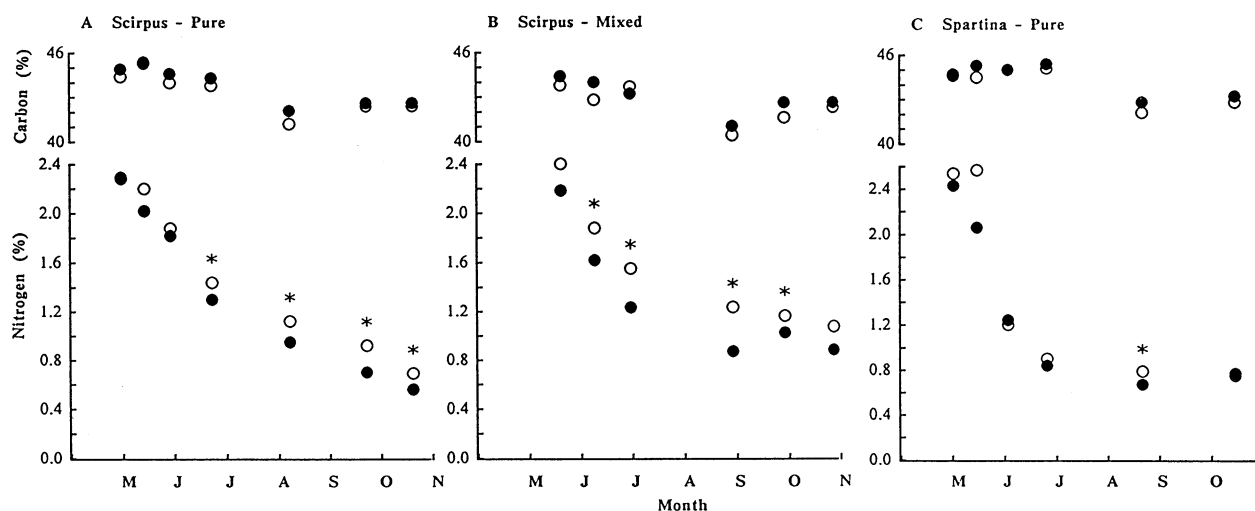


Fig. 1. A–C. Percent carbon and nitrogen in aboveground tissue from *Scirpus* growing in pure stand (A), *Scirpus* growing in the mixed community (B), and *Spartina* growing in pure stand (C) under Elevated (●) and Ambient (○) CO₂ concentrations. Asterisk indicates significant difference ($P < 0.05$) between treatments

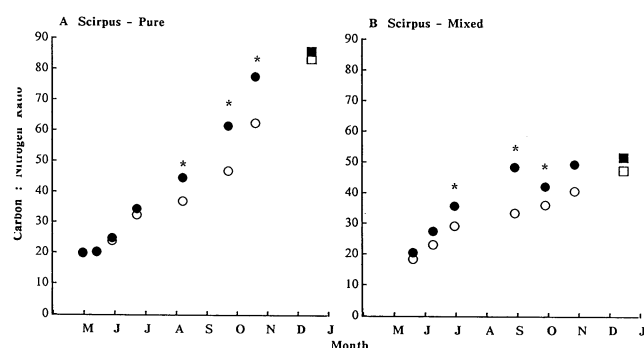


Fig. 2. A, B. Carbon: Nitrogen ratio of green (●, ○) and senescent (■, □) tissue from *Scirpus* growing in pure stand (A), and in the mixed community (B). Plants were exposed to Elevated (shaded symbols) or Ambient (open symbols) CO₂ concentrations. Asterisk indicates significant difference ($P < 0.05$) between treatments

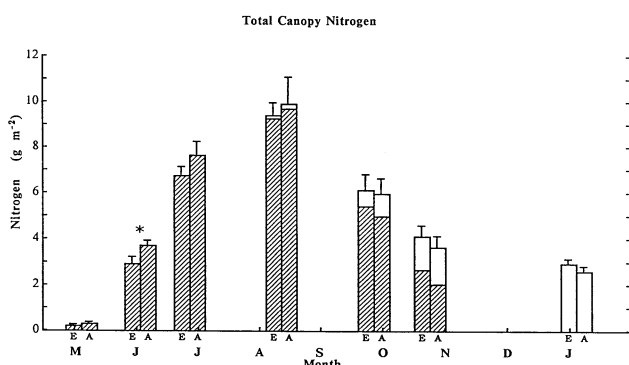


Fig. 3. Total canopy N in pure stand *Scirpus* under Elevated (E) and Ambient (A) CO₂ concentrations throughout the growing season. Total N is partitioned into that present in green tissue (shaded bars) or senescent tissue (open bars). Vertical bars indicate one standard error

Discussion

We found a clear dicotomy in the effects of elevated CO₂ on shoot %N in the C₃ and C₄ species. Increasing CO₂ reduced green tissue %N in the C₃ sedge *Scirpus olneyi* but had no effect on the C₄ grasses *Spartina patens* or *Dis-*

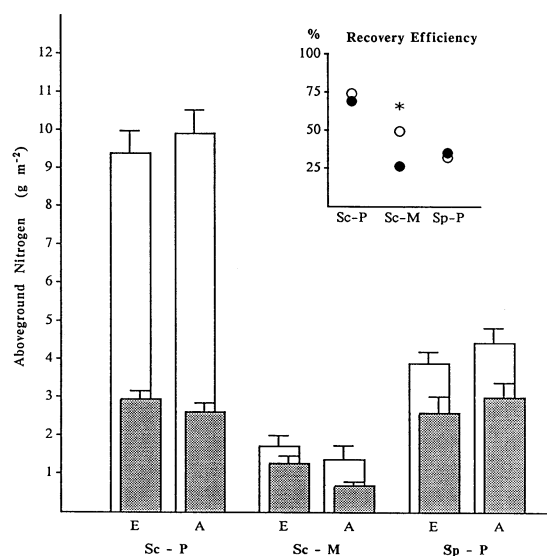


Fig. 4. Maximum aboveground N in mature tissue (open bars) and in litter (shaded bars) from *Scirpus* (Sc) and *Spartina* (Sp) canopies in pure (P) and mixed (M) communities. Vertical bars indicate one standard error. Inset, recovery efficiency of N from mature tissue under Elevated (●) and Ambient (○) CO₂ concentrations. Asterisk indicates significant difference ($P < 0.05$) between treatments

tichlis spicata. These results agree with previous studies using agricultural species grown under controlled conditions. In both soybean (Sionit 1983; Vu et al. 1983) and cotton (Wong 1979) leaf %N declined under elevated CO₂ but this was not observed in the C₄ species maize (Wong 1979). Reduced leaf %N could account for the decrease in photosynthetic capacity of high CO₂ grown plants when measured at normal ambient concentrations (von Caemmerer and Farquhar 1984). In C₃ plants, however, increased intercellular CO₂ concentrations at high CO₂ compensate for the reduction in tissue %N, resulting in higher leaf photosynthetic rates and greater productivity (Acock and Allen 1985).

Long term exposure to elevated CO₂ can cause a buildup of starch in leaves and feedback inhibition of photosyn-

Table 2. Carbon and nitrogen content of seeds and bracts from *Scirpus* growing in pure stand. Mean (\pm S.E.) $n = 5$

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

* similar superscript denotes no significant difference, $P < 0.05$

thesis (DeLucia et al. 1985). We found no evidence for increased carbon in *Scirpus* shoots although Drake et al. (1987) reported increases in both canopy and single leaf photosynthesis under elevated CO₂. This suggests that belowground rhizomes provided adequate sinks for the increased assimilation. *Scirpus* also showed no signs of photosynthetic acclimation to or inhibition by elevated CO₂ (Drake et al. 1987).

The reduction in % N of *Scirpus* shoots resulted in an increase in green tissue C/N ratios of between 20 and 40%. Insect herbivores respond to changes in the relative amount of N in leaves by altering their feeding behavior and the amount of tissue consumed (Scriber 1984). We have not observed large amounts of herbivore damage in our experimental plots but periodic outbreaks of stem borers (*Archana oblonga*) are known to occur on this marsh (T. Jordan unpublished work). On a New England salt marsh Vince et al. (1981) showed a positive relationship between insect herbivore abundance and fecundity, and plant tissue N. Soybean looper (*Pseudoplusia includens*) larvae consumed leaf tissue at 30% greater rates from high CO₂ grown soybeans than from controls because of lower leaf % N and higher specific leaf weight (Lincoln et al. 1986). A shift in insect feeding preference away from *Scirpus*, or alternatively, a greater consumption of *Scirpus* tissue to meet nutritional demands could have important consequences for plant species interactions and community composition (McBrien et al. 1983).

Seed N can vary within a species in response to local variation in nutrient availability (Parrish and Bazzaz 1985) or conditions which affect N uptake such as light and water (Khan 1982). There have been few reports on the effects of CO₂ enrichment on seed % N. Rogers et al. (1984) found a decrease in the protein content of soybean seeds under elevated CO₂ while Havelka et al. (1984) reported no effect on % N in wheat seeds. *Scirpus* appears to preferentially allocate N into seeds since both the green shoots supporting the inflorescences and the bracts enveloping the seeds had lower % N under elevated CO₂ but there was no reduction in seed % N.

Salt marsh productivity has generally been considered to be limited by N availability. Numerous field (Gallagher 1975; Mendelssohn 1979; Vince et al. 1981) and controlled environment studies (Linthurst and Seneca 1981; Morris 1982) have shown that individual species' growth, and net primary productivity increase with increasing N availability. Although *Scirpus* primary productivity increased under

elevated CO₂, we found no evidence for an increase in total aboveground N.

This has important implications for the long term responses of *Scirpus* to elevated CO₂. Photosynthesis and growth decline with declining leaf % N under a broad range of environmental conditions (Field and Mooney 1984). Reductions in N availability also reduce both the absolute and the relative increase in growth due to elevated CO₂ (Acock and Allen 1985). While results from the first year of a long term study such as this can only indicate trends in ecosystem level processes, our data suggest no net increase in N availability under elevated CO₂, with plant tissue % N declining in parallel with increases in growth. Tissue N may be reallocated to new growth as less is invested in ribulose biphosphate carboxylase under elevated CO₂. This apparent tradeoff, between new growth and tissue % N, could limit the potential for continued increases in productivity due to CO₂. We do not know, however, to what extent tissue % N was limiting this year's productivity.

Biologically fixed N may represent a source of N which could respond positively to increased photosynthetic rates under elevated CO₂. N₂ fixing bacteria isolated from within roots and rhizomes of *Spartina alterniflora* appear to benefit from plant derived photoassimilate in the form of organic acids (Boyle and Patriquin 1981). *Scirpus olneyi* collected from a population within 1 km of the present study site had root associated N₂ fixation rates 78% of those found in *S. alterniflora* (van Berkum and Slogar 1979). The biology of this association is poorly understood, however, and further work will be required before its importance to plant growth on this marsh is clear.

In perennial plants, the translocation of N from green tissue to storage organs before it is lost as litter reduces the demand on net uptake to support continued growth (Hopkinson and Schubauer 1984). The recovery efficiency of mature tissue N increases (ie. relatively more N is saved) in marsh plants as N limitation increases (Shaver and Melillo 1984). *Scirpus*, however, did not respond to the reduction in leaf % N by increasing N recovery efficiency. In pure stand, *Scirpus* had a recovery efficiency of approximately 70% – similar to the maximum of 66% reported by Shaver and Melillo (1984) for three marsh species grown at limiting available N – but there was no effect of CO₂. Recovery efficiency was lower in the mixed community where *Scirpus* was heavily shaded by *Spartina* and *Distichlis* and light may have been more important in limiting growth than N availability. Elevated CO₂ further reduced recovery efficiency in the mixed community resulting in more N lost in litter.

We found no change in the C/N ratio of litter from any community indicating that CO₂ will not affect the rate of decomposition or N mineralization (Melillo et al. 1984). As long as productivity and decomposition remain out of phase (increased productivity and constant decomposition rates), carbon accretion in communities containing *Scirpus* should increase (Oechel and Strain 1985). An increase in soil organic matter of high C/N ratio (>ca. 30) can lead to a reduction in available N through immobilization and a resultant decrease in plant growth (Stevenson 1986). This is unlikely to occur in our study area since interstitial N concentrations are high and particulate organic N is continually imported from adjacent creek water (Jordan et al. 1983). We conclude that the ability of *Scirpus* to acquire additional N from the marsh sediments, rather than a de-

cline in N availability, may ultimately limit increases in productivity in response to elevated CO₂.

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