

ELEVATED ATMOSPHERIC CO₂ EFFECTS ON BELOWGROUND PROCESSES IN C₃ AND C₄ ESTUARINE MARSH COMMUNITIES¹

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Abstract. Belowground carbon allocation is a major component of a plant's carbon budget, yet relatively little is known about the response of roots to elevated atmospheric CO₂. We have exposed three brackish marsh communities dominated by perennial macrophytes to twice ambient CO₂ concentrations for two full growing seasons using open top chambers. One community was dominated by the C₃ sedge *Scirpus olneyi*, one was dominated by the C₄ grass *Spartina patens*, and one was a mixture of *S. olneyi*, *S. patens*, and *Distichlis spicata*, a C₄ grass. Root and rhizome growth were studied in the 2nd yr of exposure by measuring growth into peat cores previously excavated and refilled with sphagnum peat devoid of roots. Growth under elevated CO₂ resulted in an 83% increase in root dry mass per core in the *Scirpus* community. Those roots were also significantly lower in percentage of nitrogen than roots from ambient-grown plants. There was no effect of elevated CO₂ on root growth or nitrogen content in the *Spartina* community or in the C₄ component of the Mixed community.

Key words: carbon dioxide; global climate change; nitrogen; roots; *Scirpus*; *Spartina*; wetlands.

INTRODUCTION

Recent work on the responses of native perennial plants to elevated CO₂ has begun to explain the ecological consequences of rising atmospheric CO₂ (Sionit et al. 1985, Norby et al. 1986, Tissue and Oechel 1987, Curtis et al. 1989a, b, Fajer et al. 1989). It has been shown that plants have a wide range of aboveground morphological and physiological responses to high CO₂. Photosynthesis, water use efficiency, and patterns of carbon allocation may all be affected. Little data is available, however, on comparable belowground responses. Carbon allocation to root growth, storage, mycorrhizal symbionts, and exudation to the rhizosphere can all be major components of the carbon economy of perennial plants (Bowen 1987). These carbon fluxes vary in magnitude both seasonally and over the course of plant growth from seedling to adult.

The size and activity of belowground carbon sinks may be important in determining the long-term responses of perennials to CO₂. For example, translocation of fixed carbon away from source tissue can reduce feedback inhibition of photosynthesis resulting from photosynthate accumulation under high CO₂ (Azcon-Bieto 1983). In addition, increased exploration of the rooting space or greater mycorrhizal activity could improve plant nutrient status and prolong or increase

the CO₂ response (O'Neill et al. 1987). Thus, it is important to examine belowground processes in order to predict ecosystem-level effects of increasing atmospheric CO₂ concentrations.

To our knowledge there have been no reports on the belowground responses to elevated CO₂ of mature perennials growing under field conditions. Based on studies of crop plants and native species grown under controlled conditions, root growth often responds at least as much, and perhaps more, to elevated CO₂ than does shoot growth. Crop plants typically show greater root growth relative to shoot growth at high CO₂, and this difference may increase with plant age (reviewed by Acock and Allen 1985). Tree seedlings (Sionit et al. 1985, Brown and Higginbotham 1986, Luxmoore et al. 1986, Norby et al. 1986), and native species (Bowman and Strain 1987, Wray and Strain 1987) also show an increase in root growth under high CO₂, even when there is a negligible shoot response (Larigauderie et al. 1988). Stimulation of root growth is not, however, always sufficient to cause an increase in root : shoot ratio, and either no change (Sionit et al. 1985) or a decrease (Wulff and Strain 1982, Tolley and Strain 1984) in this measure has been reported.

We have exposed three brackish marsh communities to twice ambient CO₂ concentrations in an effort better to understand whole plant, canopy, and ecosystem-level responses to elevated CO₂. The co-occurrence of C₃ and C₄ species, high annual productivity, and relatively short canopy make these communities excellent subjects for such studies. In this paper we report on the effects of elevated CO₂ on root and rhizome growth.

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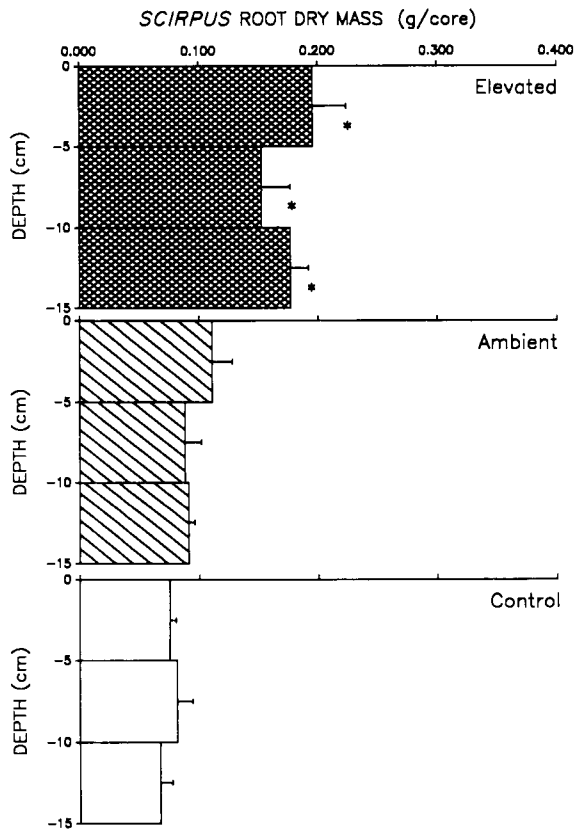


FIG. 1. Dry mass of roots recovered from regrowth cores in the *Scirpus* community under Elevated, Ambient, and Control treatments. Narrow bars indicate ± 1 SE; * $P < .05$ (significant difference between Elevated and Ambient).

MATERIALS AND METHODS

Three communities on a brackish marsh of the Rhode River, a sub-estuary of the Chesapeake Bay, were exposed to elevated CO_2 concentrations for two growing seasons beginning in April 1987. The study site and experimental design are described in Curtis et al. (1989a). One community was dominated by the perennial C_4 grass *Spartina patens* (*Spartina* community), and another by the perennial C_3 sedge *Scirpus olneyi* (*Scirpus* community). The third was a mixture of *S. patens*, *S. olneyi*, and *Distichlis spicata*, a perennial C_4 grass (Mixed community).

Within each community, 15 permanent circular plots, 0.8 m in diameter, were established along transect lines. 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 with CO_2 concentrations $\approx 338 \mu\text{L/L}$ above ambient levels (Elevated treatment), five plots had chambers receiving no additional CO_2 (Ambient treatment) and five plots had no chambers but were treated identically to chambered plots (Control treatment).

Open top chambers (0.8 m in diameter and 1.2 m in height) were used to elevate CO_2 within a plot (Drake et al. 1989). Ambient air was introduced into a chamber by a high-capacity blower and circulated within the chamber by a second blower. CO_2 was elevated within a chamber by continuously injecting 100% CO_2 into the input blower where it was mixed with ambient air before entering the chamber. Seasonal mean CO_2 concentrations (sunrise to sunset) during the 1988 growing season were $343 \pm 16 \mu\text{L/L}$ inside Ambient plots (mean \pm SD) and $681 \pm 35 \mu\text{L/L}$ inside Elevated plots. Each year treatments were begun in late April and terminated in mid- to late November.

Belowground growth was measured using regrowth cores in which the native marsh substrate was replaced after coring by a substrate lacking root material (Valiela et al. 1976, Gallagher et al. 1984). The substrate underlying these marsh communities was largely organic peat, consisting of a zone of dense roots and rhizomes (both living and dead) to a depth of ≈ 0.5 m. Below this zone the peat became progressively more decomposed and fluid in composition. One to three peat cores, 5.7 cm in diameter and 15 cm in depth, were extracted from each plot in December 1987. When more than one core was taken (i.e., plots were subsampled), results were pooled, giving a single value for each plot. In early April 1988, before aboveground growth was initiated, these excavated cores were repacked with commercial peat moss sifted to pass through a 2-mm sieve and wetted with estuarine water. No attempt was made to duplicate the bulk density of the original marsh peat. Roots and rhizomes were then allowed to grow back into this sifted peat substrate.

Regrowth cores were extracted from the plots between 30 November and 3 December 1988, using the original coring device. Cores were stored frozen until analyzed. When thawed, they were cut into 5-cm sections and all roots and rhizomes, both living and dead, were washed free of peat moss. In the Mixed community it was not possible to distinguish visually among roots of the different species. *Scirpus* rhizomes develop a red epidermis as they age and can be distinguished from the rhizomes of *Spartina* and *Distichlis*. These were referred to as the red *Scirpus* rhizome component. Newly elongated *Scirpus* rhizomes, however, could not be separated from rhizomes of the other species. All tissue was dried at 60°C , weighed, and ground to pass through a 1.0-mm screen with a Wiley mill. Nitrogen (N) and carbon (C) were analyzed with a Carbon-Hydrogen-Nitrogen analyzer (Control Equipment Corporation, Lowell, Massachusetts) at the University of Maryland, Horn Point Laboratory. Nitrogen and carbon content were calculated as percentage of dry mass. A priori pairwise comparisons (Elevated vs. Ambient, Ambient vs. Control) were made using the Least Significant Difference. All percentages and ratios were arcsine transformed before analysis to improve normality.

TABLE 1. Total root and rhizome biomass recovered from regrowth cores in the *Scirpus*, *Spartina*, and Mixed communities. Data are means ± SE. The same superscript letters indicate no significant difference within a community, *P* < .05.

Community	Elevated	Ambient	Control
Root dry mass (g/core)			
<i>Scirpus</i>	0.53 ± 0.05 ^a	0.29 ± 0.03 ^b	0.22 ± 0.02 ^b
<i>Spartina</i>	0.35 ± 0.03 ^a	0.31 ± 0.04 ^a	0.39 ± 0.02 ^a
Mixed	0.48 ± 0.04 ^a	0.40 ± 0.05 ^{ab}	0.32 ± 0.06 ^b
Rhizome dry mass (g/core)			
<i>Scirpus</i>	0.53 ± 0.27 ^a	0.87 ± 0.37 ^a	0.22 ± 0.09 ^a
<i>Spartina</i>	0.31 ± 0.08 ^a	0.21 ± 0.03 ^a	0.25 ± 0.04 ^a
Mixed-total*	0.42 ± 0.04 ^a	0.33 ± 0.04 ^a	0.32 ± 0.05 ^a
Mixed-red <i>Scirpus</i> *	0.16 ± 0.06 ^a	0.03 ± 0.03 ^b	0.03 ± 0.02 ^b

* Rhizome biomass from the Mixed community was analyzed with all species combined (Mixed-total) or just the red *Scirpus* rhizome component (Mixed-red *Scirpus*).

RESULTS

There were marked differences in root growth into regrowth cores among the three communities, both in the distribution of roots through the cores and in the response to elevated CO₂. In the *Scirpus* community, root growth was evenly distributed throughout the 15-cm profile, with no significant differences in root biomass among the 5-cm sampling intervals within a treatment (Fig. 1). Exposure to elevated CO₂ had a pronounced effect on root growth in this C₃ species, resulting in an 83% increase in total root biomass (Table 1). This additional biomass was evenly distributed throughout the core, with each 5-cm interval from Elevated chambers showing similar increases in root mass compared to cores from Ambient chambers. We found no evidence for a chamber effect (i.e., Ambient vs. Control treatments) on root growth or on the rooting profile.

In the *Spartina* community, root growth was unevenly distributed, with 70–80% of the biomass occurring in the top 5 cm and <4% occurring between 10 and 15 cm (Fig. 2). There was no response by this C₄ community to elevated CO₂, either in terms of total root biomass (Table 1) or in growth at any sampling interval (Fig. 2). There was, however, an apparent negative chamber effect, with Control plots having significantly more root biomass at 0–5 cm than Ambient plots.

The Mixed community was intermediate between the *Scirpus* and *Spartina* communities in rooting profile and response to elevated CO₂. Root growth was unevenly distributed, but with a greater fraction (6–15%) occurring between 10 and 15 cm than was found in the *Spartina* community (Fig. 3). Total root biomass was not affected by CO₂ (Table 1) but this was due to a lack of response by the majority of roots growing in the upper 10 cm. Between 10 and 15 cm, where *Scirpus*

roots should predominate, there was a 165% increase in root growth in Elevated vs. Ambient chambers. We found no evidence for a significant chamber effect on root growth.

Elevated CO₂ had no effect on total rhizome dry mass per core in any of the three communities (Table 1). Presence of *Scirpus* rhizomes in the cores was highly variable, with coefficients of variation ranging between 84 and 224%. In the Mixed community, while there was no CO₂ effect on total rhizome growth (C₃ plus C₄), there was a greater than fivefold increase in older *Scirpus* rhizomes under elevated CO₂. In this case the magnitude of the effect was sufficient to offset high variability in rhizome recovery. Root biomass was approximately equal to rhizome biomass in each community (Table 1). High variability in the rhizome data was sufficient, however, to obscure any significant CO₂ effect on the combined root plus rhizome biomass (data not shown).

Root % N was significantly lower in the *Scirpus* community under elevated CO₂ (Fig. 4A) while % C remained unchanged (Fig. 4B). This resulted in an increase in the C/N ratio of *Scirpus* root tissue of 22%

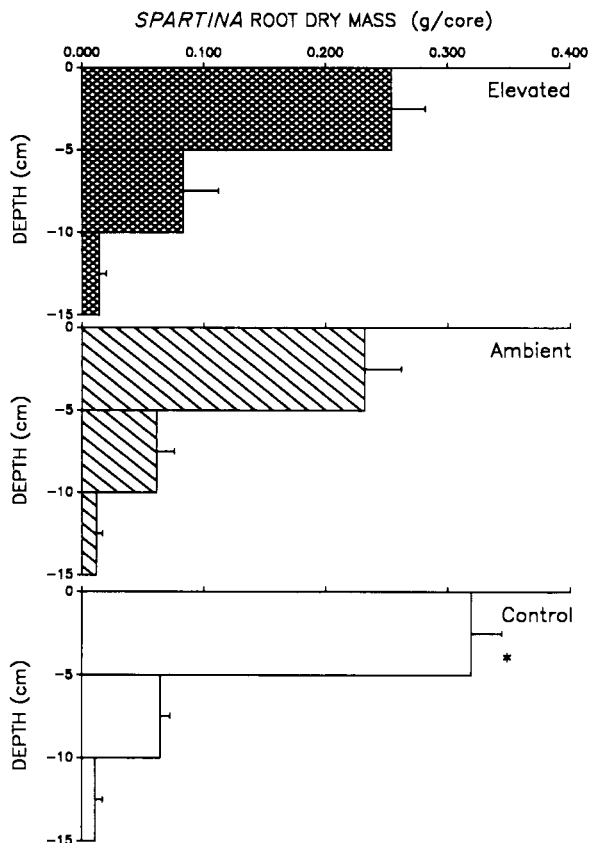


FIG. 2. Dry mass of roots recovered from regrowth cores in the *Spartina* community under Elevated, Ambient, and Control treatments. Narrow bars indicate +1 SE; **P* < .05 (significant difference between Ambient and Control).

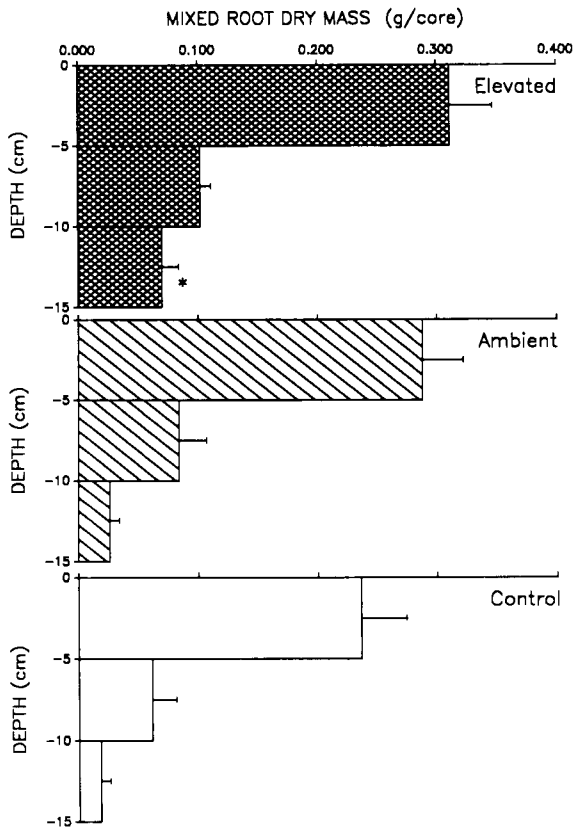


FIG. 3. Dry mass of roots recovered from regrowth cores in the Mixed community under Elevated, Ambient, and Control treatments. Narrow bars indicate ± 1 SE; * $P < .05$ (significant difference between Elevated and Ambient).

(Fig. 4C). Elevated CO_2 had no effect on the N or C content of roots from the *Spartina* community. Roots from the Mixed community had slightly lower % N ($P < .10$) and higher C/N ratio ($P < .12$) under elevated CO_2 .

DISCUSSION

Increased allocation of carbon to belowground structures under elevated CO_2 concentrations has been a common observation in both agricultural and native species (Sionit et al. 1985, Luxmoore et al. 1986, Bowman and Strain 1987, Larigauderie et al. 1988). Generally, however, the plants under consideration have been annuals, seedlings, or cuttings of perennial species grown under controlled conditions. Our results show that root growth can constitute an important sink for fixed carbon in mature, perennial species growing under twice ambient CO_2 in the field.

In a community dominated by the C_3 sedge *Scirpus olneyi*, elevated CO_2 significantly increased root growth during the main growing season between April and December. Our estimates of growth were probably conservative, since regrowth cores tend to underestimate actual belowground production (Valiela et al. 1976,

Gallagher et al. 1984). Since our observations were limited to the top 15 cm of peat, these data cannot be used to calculate total belowground root biomass. However, *Scirpus* roots between 10 and 15 cm depth responded just as strongly to CO_2 as did surface roots (Fig. 1) suggesting no differential response with depth. Our data are therefore consistent with other observations on entire root systems showing an increase in root growth under elevated CO_2 .

Although we could not separate *Scirpus* roots from the roots of *Spartina* and *Distichlis*, a comparison of the rooting profiles in the *Spartina*, *Scirpus*, and Mixed communities indicated an increase in root growth by *Scirpus* in the Mixed community as well. In the *Spartina* community there was little root growth between 10 and 15 cm, while in the *Scirpus* community root biomass at that depth represented 34% of the total growth. It was only between 10 and 15 cm in the Mixed

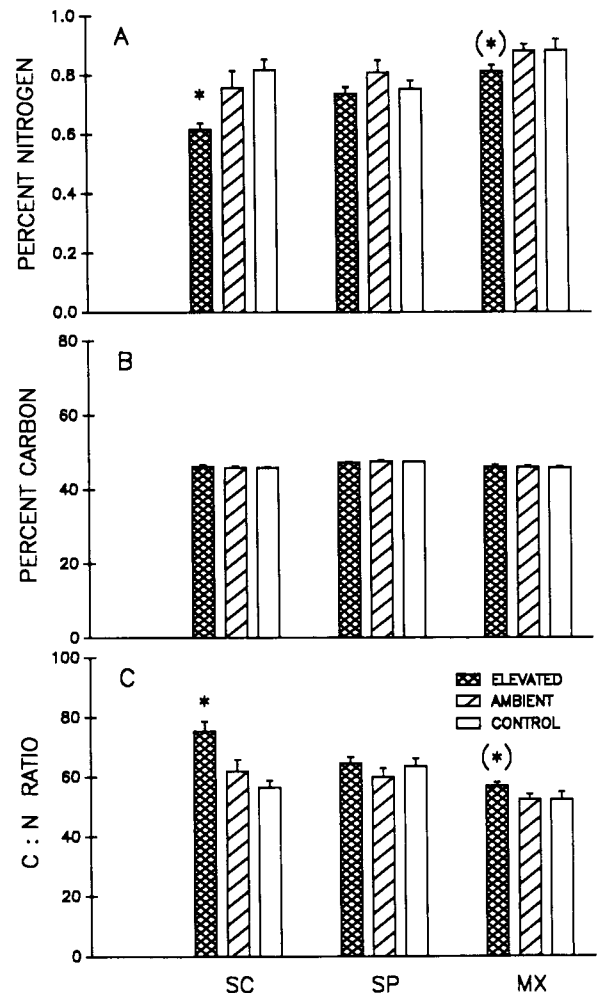


FIG. 4. Nitrogen (A) and carbon (B) content and carbon : nitrogen ratio (C) of roots from the *Scirpus* (SC), *Spartina* (SP), and Mixed (MX) communities exposed to Elevated, Ambient, and Control conditions. Narrow vertical bars indicate 1 SE; significance levels are: * $P < .05$, (*) $P < .12$.

community that we found a significant, and large (165%), increase in root growth in response to CO₂. The presence of *Spartina* and *Distichlis* roots could have changed the rooting profile of *Scirpus* relative to what was found in the pure community by, for example, excluding *Scirpus* roots from the upper 10 cm. This might have exaggerated the CO₂ response at 10–15 cm relative to the pure *Scirpus* community. Nonetheless, given the lack of any previous growth response to CO₂ by the C₄ species (Curtis et al. 1989a), and the observed rooting profiles in pure *Scirpus* and *Spartina* communities, the positive CO₂ response in the Mixed community at 10–15 cm is best explained as growth by *Scirpus* roots.

A primary effect of CO₂ on *Scirpus* aboveground growth in both pure and Mixed communities was an increase in shoot density (Curtis et al. 1989a). Shoot density and rhizome growth were strongly correlated in *Scirpus americanus* (Giroux and Bedard 1987), and we had also predicted an increase in *Scirpus* rhizome growth under elevated CO₂. Our inability to detect such an effect may be due to the high variability in recovery of *Scirpus* rhizomes in regrowth cores (Table 1). *Scirpus* rhizomes were larger and more widely spaced in the marsh peat relative to the regrowth core diameter than were *Spartina* rhizomes and sampling variability was consequently larger. In the Mixed community, increases in *Scirpus* aboveground NPP under elevated CO₂ were much greater (234%). This large CO₂ effect on shoot growth was reflected in a measurable, and significant, increase in rhizome growth, despite high variability in rhizome recovery (Table 1).

In contrast to the increase in *Scirpus* root and rhizome growth under elevated CO₂ there were no belowground responses to CO₂ in the *Spartina* community or in the C₄ component of the Mixed community. These results are consistent with the overall lack of response to elevated CO₂ in either shoot density or aboveground NPP by *Spartina* or *Distichlis* (Curtis et al. 1989a). As a group, C₄ species respond less to elevated CO₂ than do C₃ species, although positive growth responses have been reported (Wong 1979, Carlson and Bazzaz 1980, Bowman and Strain 1987).

Root tissue % N decreased and the C/N ratio increased in the *Scirpus* community under elevated CO₂ (Fig. 4). Similar results had been found previously in *Scirpus* shoot tissue (Curtis et al. 1989b). Such changes in elemental composition can have significant effects on herbivore preference and feeding rates (Lincoln et al. 1986, Fajer et al. 1989). While root herbivores are probably not abundant in anaerobic peat, these changes in tissue composition could influence decomposition rates. Increasing tissue C/N ratio decreases the decomposition rate (Melillo et al. 1984, Taylor et al. 1989). Greater root growth combined with slower decomposition would tend to increase carbon accretion and peat formation in wetland communities containing *Scirpus olneyi*.

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