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Interactions between C₃ and C₄ salt marsh plant species during four years of exposure to elevated atmospheric CO₂

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Abstract

Elevated atmospheric CO₂ is known to stimulate photosynthesis and growth of plants with the C₃ pathway but less of plants with the C₄ pathway. An increase in the CO₂ concentration can therefore be expected to change the competitive interactions between C₃ and C₄ species. The effect of long term exposure to elevated CO₂ (ambient CO₂ concentration + 340 μmol CO₂ mol⁻¹) on a salt marsh vegetation with both C₃ and C₄ species was investigated. Elevated CO₂ increased the biomass of the C₃ sedge *Scirpus olneyi* growing in a pure stand, while the biomass of the C₄ grass *Spartina patens* in a monospecific community was not affected. In the mixed C₃/C₄ community the C₃ sedge showed a very large relative increase in biomass in elevated CO₂ while the biomass of the C₄ species declined.

The C₄ grass *Spartina patens* dominated the higher areas of the salt marsh, while the C₃ sedge *Scirpus olneyi* was most abundant at the lower elevations, and the mixed community occupied intermediate elevations. *Scirpus* growth may have been restricted by drought and salt stress at the higher elevations, while *Spartina* growth at the lower elevations may be affected by the higher frequency of flooding. Elevated CO₂ may affect the species distribution in the salt marsh if it allows *Scirpus* to grow at higher elevations where it in turn may affect the growth of *Spartina*.

Nomenclature: Radford, A. E., Ahles, H. E. & Bell, C. R. (1968). Manual of the vascular flora of the Carolinas, University of North Carolina Press, Chapel Hill.

Introduction

The atmospheric CO₂ concentration is increasing due to the burning of fossil fuels and deforestation, and is expected to double in the next century relative to pre-industrial levels (Strain & Cure 1985). The present atmospheric CO₂ concentration (ca 353 μmol mol⁻¹) is a limiting factor to photosynthesis of plants with the C₃ pathway. Consequently, an increase in the CO₂ concentra-

tion enhances photosynthesis and productivity in these plants (Cure & Acock 1986). Because of the CO₂ concentrating mechanism of the C₄ pathway, photosynthesis of C₄ plants is much less limited by the ambient CO₂ concentration. All plants can benefit by elevated CO₂ by regulating the stomatal conductance and limiting water loss through evapotranspiration. In plant communities containing both C₃ and C₄ species the relative advantage of the C₃ species in high CO₂ may

alter the competitive balance in favor of the C₃ species, as long as other abiotic factors (e.g. temperature) do not change. An increased competitive ability of C₃ species growing with C₄ species has been found in competition experiments (Carter & Peterson 1983; Bazzaz & Carlson 1984; Patterson *et al.* 1984; Zangerl & Bazzaz 1984; Marks & Strain 1989), although an increase in the competitiveness of the C₄ species in elevated CO₂ has also been reported (Bazzaz *et al.* 1989). Not all C₃ species show the same response to elevated CO₂, and therefore changes in the competition between C₃ species in high CO₂ may also occur (Garbutt & Bazzaz 1984; Tolley & Strain 1984a; Tolley & Strain 1984b; Overdieck & Reining 1986).

If elevated CO₂ can prevent the C₃ species from declining during drought stress relative to the C₄ species, then the relative advantage of elevated CO₂ to C₃ species may be as large during drought stress as during periods with sufficient rainfall.

Most studies on the effect of elevated CO₂ on competition between C₃ and C₄ species have been conducted in greenhouse or growth chamber, and were limited to one season or less. Growing plants in small pots may affect the competition experiments because this affects the response of plants to elevated CO₂ by limiting the sink for photosynthates (Arp 1991). Long term CO₂ exposure experiments on natural vegetation containing C₃ and C₄ species have not yet been described. This paper describes the effects of four years of exposure to elevated CO₂ on the competition between C₃ and C₄ perennial species in a natural salt marsh ecosystem.

In this ecosystem species are distributed in very distinct patterns. The C₃ sedge *Scirpus olneyi* and the C₄ grass *Spartina patens* occur in almost pure stands, as well as in a mixed community with the C₄ grass *Distichlis spicata*. Interspecific relationships and the effects of abiotic factors on species distribution need to be understood before predictions can be made on the impact of elevated CO₂ on the distribution of the species in the salt marsh (Rozema *et al.* 1991b; Rozema *et al.* 1988). The elevation of the marsh may be the most important abiotic variable affecting species distribution be-

cause plants at higher elevations are more subject to drought and fluctuations in salinity. At lower elevations the increased frequency and duration of flooding results in more anaerobic conditions and lower redox potentials in the soil, which can reduce the growth of plants not equipped with a well-functioning aerenchyma system (Rozema *et al.* 1988; Van Diggelen 1988; Ernst 1990).

Materials and methods

CO₂ exposure system

The effects of long term exposure to elevated CO₂ on three salt marsh communities were investigated in a subestuary of the Chesapeake Bay, USA. The first community was dominated by the C₃ sedge *Scirpus olneyi*, the second community was a monospecific stand of the C₄ grass *Spartina patens*, and the third community consisted of a mixture of *Scirpus*, *Spartina* and another C₄ grass, *Distichlis spicata*. Ten open top chambers were placed in each community. In five chambers plants were exposed to normal ambient CO₂ concentration (350 μmol CO₂ mol⁻¹ air), and in the other five chambers the CO₂ concentration was raised 340 μmol mol⁻¹ above the ambient CO₂ concentration. The plants were exposed to elevated CO₂ from 1987 to 1990. The CO₂ exposure started when plants emerged in the spring and ended after total senescence in the fall. Five sites without chambers in each community were used as controls. For a detailed description of the CO₂ exposure and measurement system see Drake *et al.* (1989).

Biomass estimation

Aboveground biomass of *Scirpus*, *Spartina* and *Distichlis* in all chambers and control sites was estimated in June 1986 before the CO₂ treatment started, as well as seven times during the growing season of 1987, five times during 1988, and once at peak biomass in 1989 and 1990. *Scirpus* shoots are unbranched and lack leaves, allowing

for non-destructive biomass estimation using the relationship between shoot length and dry weight. A small sample of shoots ($\pm 3\%$) was harvested to determine this relationship, while the length of all other shoots in the chambers was measured. In 1989 and 1990 the regression was improved by measuring both shoot length and shoot width at a height of 40 cm. Total biomass was calculated by applying the regression to the length measurements of all shoots in the chambers. From 1986 to 1988 *Spartina* and *Distichlis* biomass was estimated by harvesting 5 quadrats of $5 \times 5 \text{ cm}^2$ from each chamber to establish the dry weight per shoot, and counting the shoots in 5 quadrats of $10 \times 10 \text{ cm}^2$ to estimate the density of the shoots. Total biomass was calculated by extrapolating the shoot density and shoot weight measurements. In 1989 and 1990 biomass was estimated by harvesting 10 to 12 quadrats of $5 \times 5 \text{ cm}^2$ from each chamber and extrapolating the results to total biomass per meter squared. Senescence and percentage of shoots which were reproductive were also recorded for all species.

Water relations

Midday and pre-dawn water potential measurements were made several times during the grow-

ing season using a Scholander pressure bomb. Soil salinity measurements were made with a refractometer, using interstitial water obtained from pvc pipes 15, 30, 50 and 100 cm deep, which were installed in six chambers of each community in 1987. Rainfall and temperature data were recorded at the Smithsonian Environmental Research Center, approximately 1.5 km from the study site.

Marsh survey

The elevation of the marsh was measured in 1990 by establishing the height of points in a grid over a $130 \times 80 \text{ m}$ area using a surveyors level (Keuffel & Esser). A $5 \times 5 \text{ m}$ grid was laid out over the study site and 3 measurements were taken at each point, 50 cm apart. The composition of the vegetation and the average height of the *Scirpus* shoots were also estimated at these points.

To determine the effect of *Scirpus* canopy on the light environment of *Spartina*, photosynthetic photon flux (PPF) was measured using a sunfleck septometer (Decagon) at 25, 50, 75, 100 and 125 cm above the surface of the marsh over an 10 m transect extending from the *Spartina* to the *Scirpus* community. *Scirpus* shoot density and shoot height were also recorded over this transect.

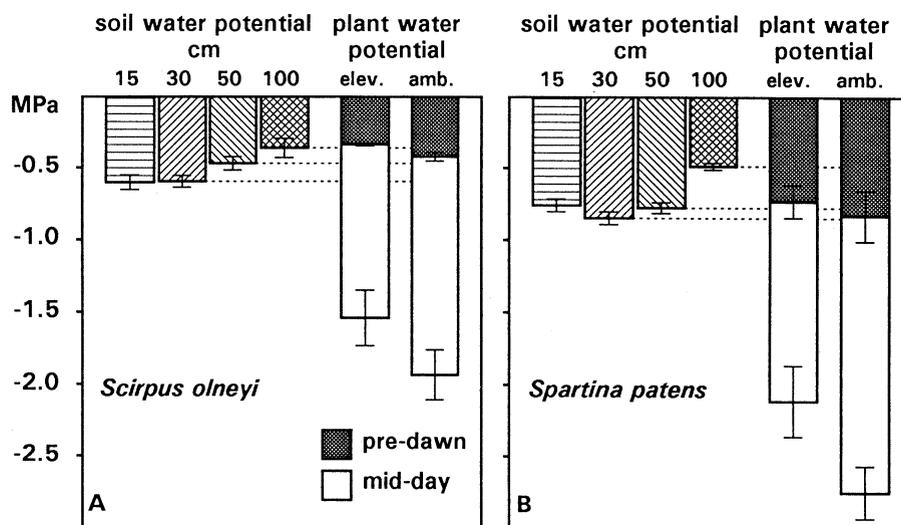


Fig. 1. Soil water potential at four different depths, and plant water potential measured mid-day and pre-dawn for plants grown at elevated and ambient CO_2 . A: *Scirpus olneyi*, B: *Spartina patens*.

Results and discussion

Water relations of Scirpus olneyi and Spartina patens

Pre-dawn and mid-day plant water potentials of *Scirpus* and *Spartina* were measured six times in the period June to August 1988, and mean values for plants grown in elevated and ambient CO₂ are presented in Fig. 1. Water potential of both *Scirpus* and *Spartina* grown in elevated CO₂ was ± 0.6 MPa higher (less negative) than plants grown in ambient CO₂ when measured in the afternoon. Similar results have been reported for the European salt marsh species *Scirpus maritimus* (C₃), *Elymus athericus* (C₃) and *Spartina anglica* (C₄) (Lenssen & Rozema 1990; Lenssen *et al.* 1991; Rozema *et al.* 1991a; Rozema *et al.* 1991b). A smaller difference was observed between the pre-dawn water potentials. The mean salinity of interstitial water in the soil at four different depths is shown in the same figure. Soil salinity was highest in the top 30 cm of the marsh, and lowest at a depth of 100 cm. The pre-dawn water potential of *Scirpus* equilibrated at a level equal to the soil water potential at 100 cm, indicating that this species is able to tap the relatively fresh water from this level. *Spartina* pre-dawn water potential is equivalent to the soil water potential at the surface of the marsh. *Spartina* has a shallow rooting system while roots of *Scirpus* extend much deeper into the marsh (Curtis *et al.* 1990).

Spartina patens and *Distichlis spicata* have salt glands in the leaves with which they can excrete excess salt and these species can tolerate high salinity levels. *Scirpus olneyi* does not have salt glands and must rely on restricting salt uptake by the roots. Runoff from the surrounding forest may create a flow of fresh water under areas of the salt marsh which may be available to *Scirpus*, but no data are available. At the higher elevations of the marsh growth of *Scirpus* may be limited because salt and drought stress are likely to be greater than at the lower elevations during periods of drought.

If elevated CO₂ can enhance the water use efficiency of *Scirpus*, then this might improve growth

and competitive ability of *Scirpus*. Salt tolerance of C₃ species may be enhanced at elevated CO₂ by an increase in available photosynthates and by improved water status (Bowman & Strain 1987; Rozema *et al.* 1990). During dry years both C₃ and C₄ species can benefit from reduced evapotranspiration at elevated CO₂, and the relative advantage of the C₃ species in high CO₂ may be reduced. However, drought stress is likely to enhance the competitive ability of C₄ species at normal atmospheric CO₂ concentration because of their inherent higher water use efficiency, and elevated CO₂ may reduce this advantage of the C₄ species during drought by increasing the water use efficiency of the C₃ species.

The effect of elevated CO₂ on growth of Scirpus olneyi

A summary of the effects of elevated CO₂ on *Scirpus olneyi* growth in pure and mixed communities is given in Fig. 2. The data are expressed as percent increase in plants grown in elevated CO₂ when compared with plants grown in ambient CO₂ at peak biomass for four years. Shoot density increased in all four years and in both communities, but the increase was much larger in the mixed community. Shoot height decreased in the C₃ community and increased in the mixed community. The dry weight per unit shoot length was slightly enhanced during the first years but decreased in the last year. Changes in shoot density, shoot height and weight per unit shoot length were reflected in the change in total biomass. Biomass was enhanced in the C₃ community in 1987 and 1988, but showed only a small increase in 1989 and 1990. In the mixed community a large increase in *Scirpus* biomass was found in all four years, but the response in 1990 was smaller than in the other years. Elevated CO₂ reduced senescence of *Scirpus*, with the exception of the last two years in the mixed community. The percentage shoots which were flowering was reduced in elevated CO₂ during the first two years, but was enhanced in the last two years.

A large interaction of community type with el-

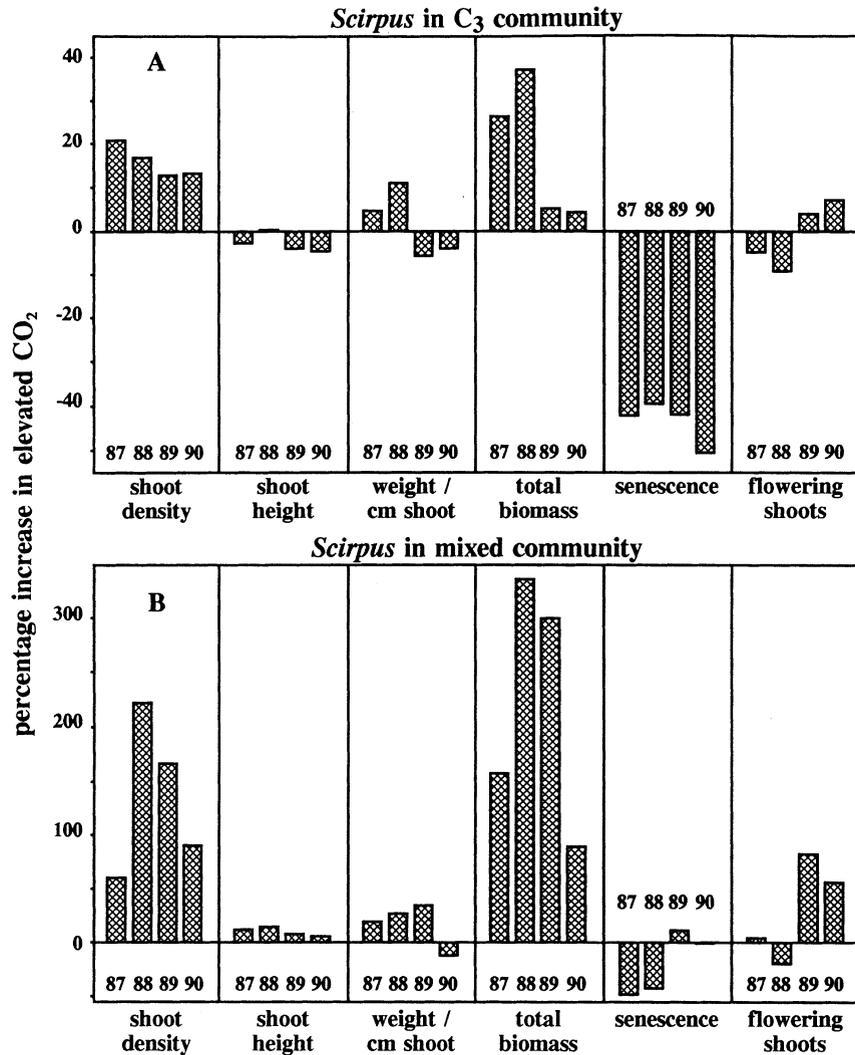


Fig. 2. Percentage increase in shoot density, shoot height, weight per unit shoot length, total biomass, senescence and reproduction of *Scirpus olneyi* plants exposed to elevated CO₂, as compared with plants grown in normal ambient CO₂ for four years. A: Pure *Scirpus olneyi* (C₃) community, B: mixed (C₃-C₄) community.

evated CO₂ was observed, with *Scirpus* in the mixed community responding much stronger to elevated CO₂ in shoot density, shoot height and biomass (Fig. 2). A possible explanation is that *Scirpus* growing in the mixed community constitutes only a small portion of the biomass and is able to expand, but when growing in the pure *Scirpus* community, the increase in biomass is restricted by intraspecific competition and self-shading. This response is similar to the findings of Carter and Peterson (1983) where *Sorghum*

responded to elevated CO₂ in the high light environment of the mixed community, but was limited in its response by self-shading in the unmixed culture.

Yearly differences in the response to elevated CO₂ were found. The increase in biomass of *Scirpus* in the pure community was much larger in the first two years, while reproduction was enhanced in the last two years. In the mixed community senescence was reduced in 1987 and 1988, and reproduction was increased in 1989 and 1990. A

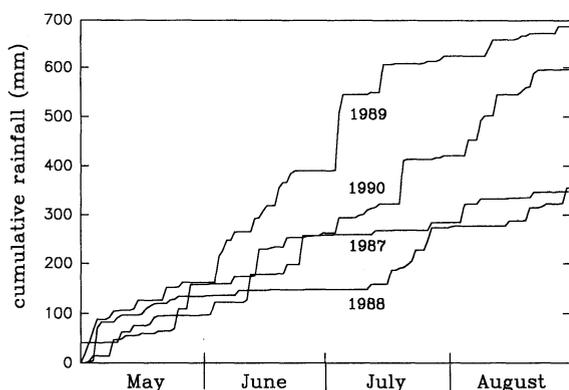


Fig. 3. Cumulative rainfall for May through August for 1987, 1988, 1989 and 1990.

drop in shoot density and biomass was also observed from 1988 to 1990. The temperature during the growing seasons of 1987 and 1988 was higher than during the last two years (mean max-

imum daytime temperature May–August: 1987: 28.8, 1988: 28.4, 1989: 26.6, 1990: 26.6 °C), and long periods of drought occurred in the first two years (Fig. 3). Rainfall deficit during the growing season has been correlated with variation in peak biomass of salt marsh plants, through its impact on soil salinity and soil moisture content (De Leeuw *et al.* 1990). In dry years, elevated CO₂ may prevent the reduction of biomass through drought, resulting in a large relative increase in biomass compared with years of abundant rainfall. In the mixed community the correlation between drought and the effect of elevated CO₂ on biomass is less clear. It is likely that the large increase in biomass in 1988 carries over into the biomass increase found in 1989. Because the effect of elevated CO₂ on growth is strongly correlated with air temperature (Idso *et al.* 1987), higher temperatures in 1987 and 1988 may also have contributed to the larger CO₂ effect.

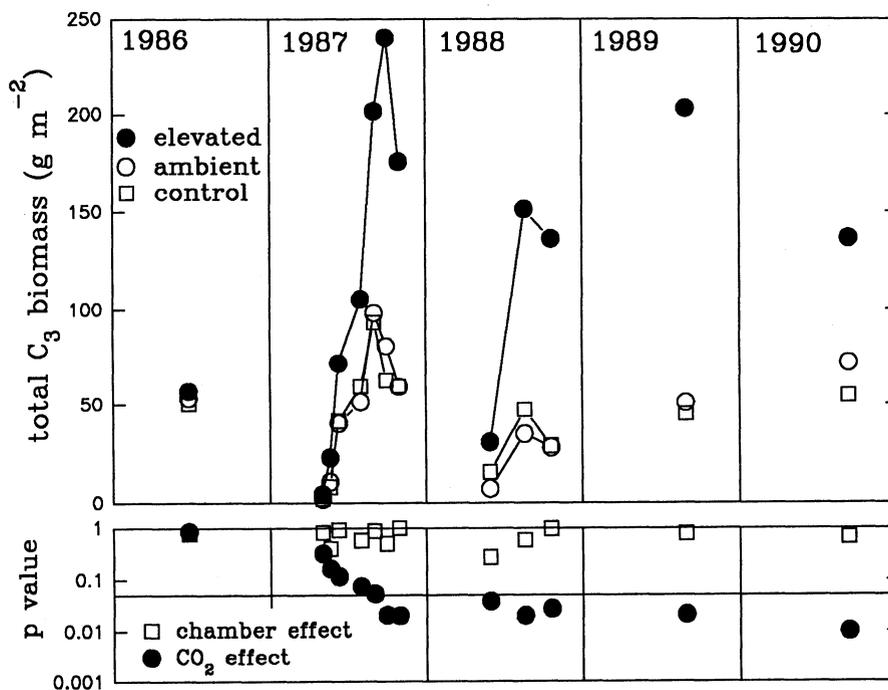


Fig. 4. A: Total biomass of *Scirpus olneyi* in the mixed community of *Scirpus*, *Spartina* and *Distichlis* for all harvests from 1986 to 1990. CO₂ treatment started in 1987. Values shown are mean values for 5 chambers. B: p-values for the difference between elevated and ambient chambers (treatment effect) and between ambient chambers and control sites (chamber effect). The horizontal line represents the 0.05 level.

The effect of elevated CO₂ on interaction between the C₃ and C₄ species

A five year record of biomass of *Scirpus* growing in the mixed community is presented in Figure 4. The mean biomass for 5 chambers of each treatment is given for every harvest since the start of the experiment. From the first year of exposure until 1990, the biomass of *Scirpus* grown in elevated CO₂ has been higher than the biomass of plants grown in ambient CO₂, and this difference became statistically significant in late 1987. A large decrease in biomass of *Scirpus* in ambient chambers and unchambered control sites of the mixed community was found from 1987 to 1988. This may have been the result of the continued drought in 1988 (Fig. 3). The decrease is smaller in *Scirpus* grown in elevated CO₂, resulting in a large relative increase in density and biomass in 1988 (Fig. 2). Biomass of *Scirpus* plants not exposed to elevated CO₂ recovered during 1989 and

1990 and the relative increase in density and biomass of plants grown in elevated CO₂ declined since 1988. However, due to a smaller variation in the data the level of significance has increased since the start of exposure to CO₂ for both shoot density and biomass (Fig. 4).

The effects of elevated CO₂ on the biomass of the C₄ grasses are presented in Figure 5. Biomass and shoot density of the C₄ species combined were lower in the elevated CO₂ chambers than in the ambient chambers in 1989 and 1990, and the effect on biomass was significant at the 0.05 level in 1990. No effect of the ambient CO₂ chamber on density or biomass was found when compared with control sites without chambers.

While density and biomass of the two C₄ grasses combined were uniform throughout the community, the distribution of each separate species in the mixed community was highly variable, obscuring any effects of elevated CO₂ on density and biomass of *Spartina* and *Distichlis* separately.

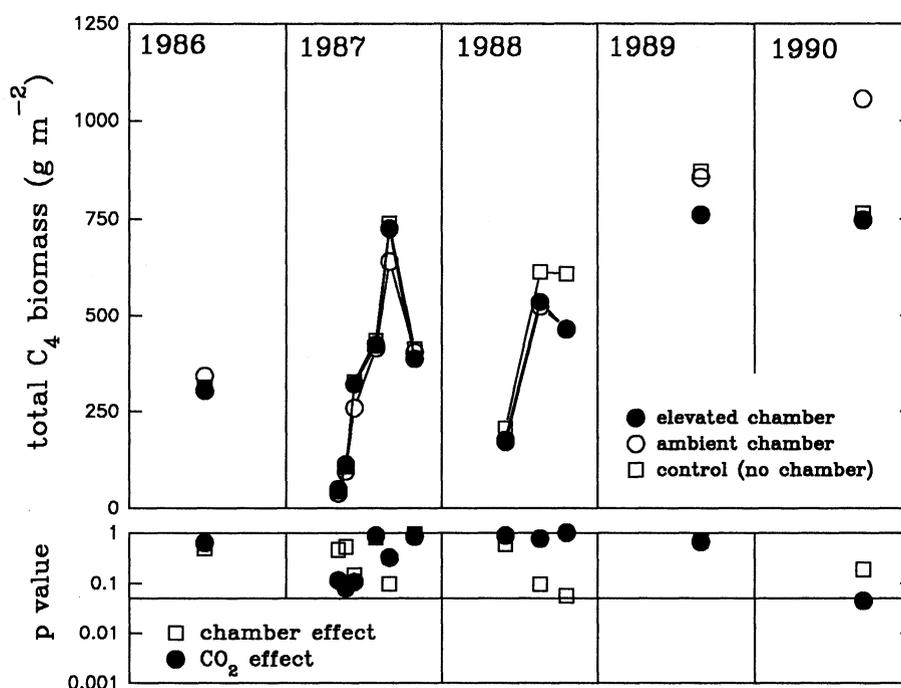


Fig. 5. A: Total biomass of the C₄ grasses *Spartina patens* and *Distichlis spicata* in the mixed community of *Scirpus*, *Spartina* and *Distichlis* for all harvests from 1986 to 1990. CO₂ treatment started in 1987. Values shown are mean values for 5 chambers. B: p-values for the difference between elevated and ambient chambers (treatment effect) and between ambient chambers and control sites (chamber effect). The horizontal line represents the 0.05 level.

However, the decline of the C₄ species in elevated CO₂ appears to be at the expense of *Spartina*, which experienced a relative decline in the biomass in elevated chambers, while the *Distichlis* biomass increased in elevated CO₂ in the first three years (Fig. 6). The reduction of C₄ biomass in the elevated chambers is larger than the increase in *Scirpus* biomass in those chambers, resulting in a lower total biomass in the elevated chambers. It has been found before that production of mixed stands may not increase with elevated CO₂, because the increase in C₃ biomass can be offset by a decrease in the C₄ biomass (Carter & Peterson 1983). With the exception of the year 1990, elevated CO₂ did not reduce the biomass of *Spartina* growing in the pure C₄ community (Fig. 6), suggesting that the decline in the mixed community may have been the result of increased competition by *Scirpus*.

The possible effects of elevated CO₂ on species distribution

The studied plant communities, while irregularly shaped, formed well defined patches. Although

only a 15 cm difference was found between the elevations where *Spartina* and *Scirpus* were most abundant, the distribution was highly correlated with the elevation of the marsh (Fig. 7). *Scirpus olneyi* reached its highest density at the lower elevations of the study site, while *Spartina patens* dominated the higher elevations. No correlation of *Distichlis spicata* with elevation was found. *Typha angustifolia* and *Iva frutescens* (data not shown) also occurred at lower elevations. *Spartina patens* is well adapted to periods of high salinity at the higher elevations, but appears to be sensitive to frequent flooding at the lower areas (Bertness 1991a; Bertness 1991b). The well developed aerenchyma of *Scirpus olneyi* provides oxygen in the waterlogged soils and allows it to grow in the lower areas of the marsh.

The effect of marsh elevation on *Scirpus* shoot height is displayed in Figure 8. A marked decline in *Scirpus* height occurred at the same elevation where biomass and shoot density of *Scirpus* were reduced and where *Spartina* became the dominant species (Fig. 7). Under favorable conditions *Scirpus* grows much taller than *Spartina* and *Distichlis* and may shade these grasses. A 10 m transect from the *Spartina* to the *Scirpus* commu-

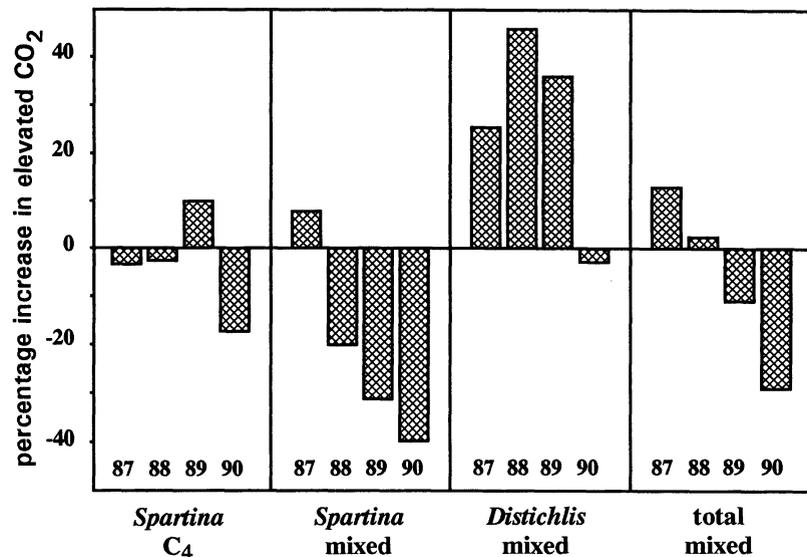


Fig. 6. Percentage increase in total biomass of plants grown in elevated CO₂ as compared with plants grown in ambient CO₂ for four years, for *Spartina patens* in the pure *Spartina* community (C₄), and for *Spartina*, *Distichlis spicata* and both C₄ species in the mixed (C₃-C₄) community.

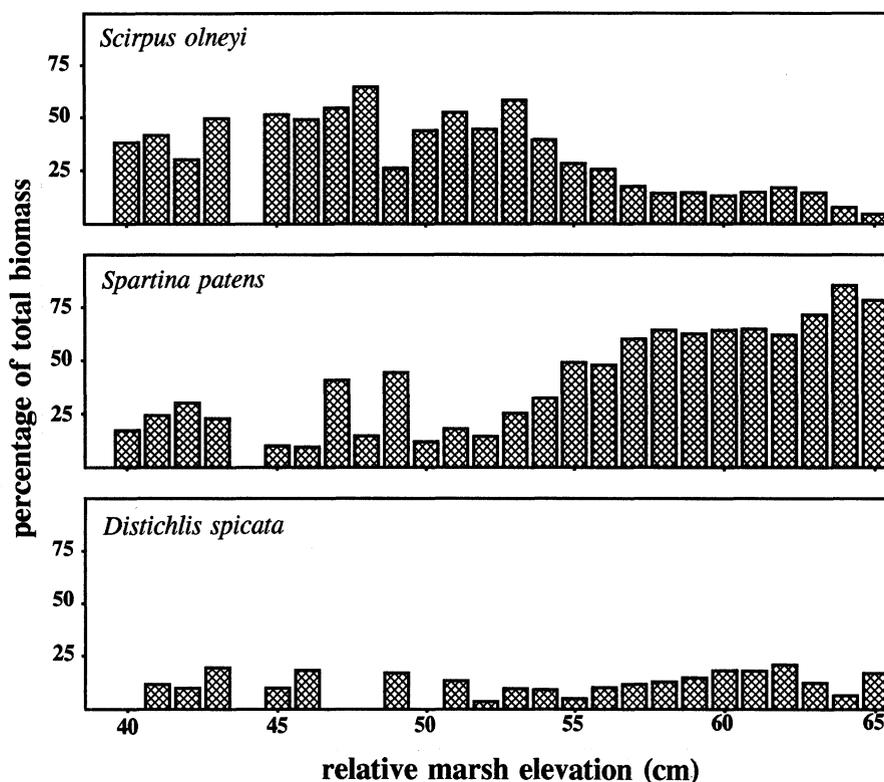


Fig. 7. Percentage of total biomass of *Scirpus olneyi*, *Spartina patens* and *Distichlis spicata* as a function of marsh elevation. *Iva frutescens* and *Typha angustifolia* were also found at the lower elevations.

nity revealed that light levels at the height of the *Spartina* canopy (± 25 cm above the surface) declined to about 20% full sunlight in the *Scirpus* community. Light intensity is likely to have a large effect on the growth of these C_4 species in the marsh because plants with the C_4 pathway can benefit more from high light levels (Ehleringer 1978). Shading by *Juncus gerardi* affected growth of *Spartina patens* in a New England salt marsh (Bertness 1991a). It can be speculated that in a high CO_2 environment an increased carbon uptake and improved salt and drought tolerance of the C_3 species *Scirpus olneyi* will allow it to expand towards higher elevations of the marsh, which may lead to a decrease of the C_4 species due to increased shading by *Scirpus*.

Conclusions

Elevated CO_2 increased the shoot density and total biomass of the C_3 sedge *Scirpus olneyi* in

both mixed and pure communities, but the increase was much larger in the mixed community with *Spartina patens* and *Distichlis spicata*. The absence of a large increase in biomass in the pure C_3 community may be explained by an increase in self shading, counteracting the effects of elevated CO_2 . This negative feedback was absent in the mixed community where *Scirpus* constituted only 5 to 10% of the total biomass and was able to expand.

It has been suggested that during periods of drought stress both C_3 and C_4 species are expected to benefit from elevated CO_2 by reducing water loss, resulting in a smaller relative benefit for the C_3 species (Pearcy & Björkman 1983; Bazzaz *et al.* 1985). In this study however, elevated CO_2 offered only a minor benefit for the drought and salt tolerant C_4 species during drought stress, but it had a large impact on the C_3 species. At high CO_2 the C_3 sedge was able to maintain its position in the community, while bio-

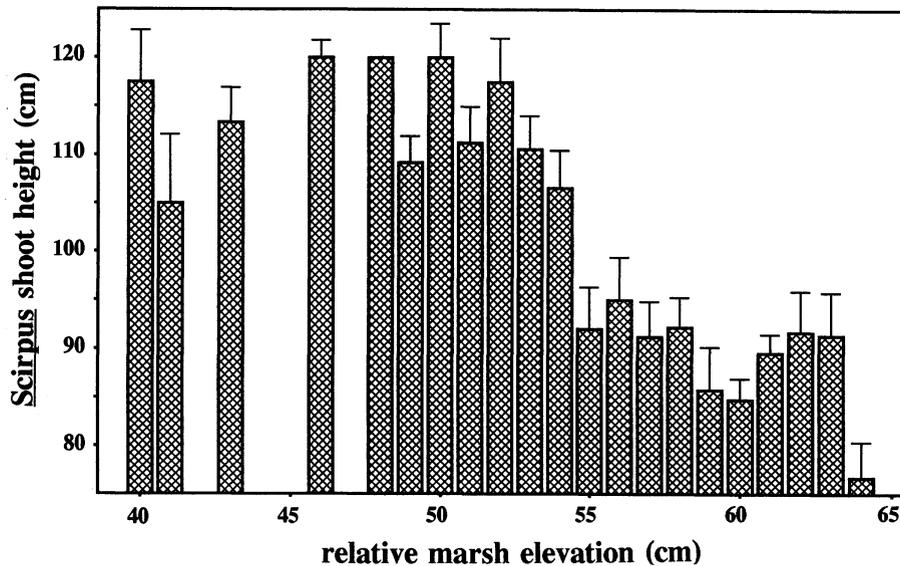


Fig. 8. Mean shoot height of *Scirpus olneyi* as a function of marsh elevation.

mass was reduced by drought at ambient CO₂ levels. As a result drought stress amplified the difference between C₃ and C₄ species in response to elevated CO₂. A similar response to drought was found in the pure C₃ community where elevated CO₂ increased biomass in the two dry years, but in the years with abundant rainfall biomass was only marginally increased by elevated CO₂.

The increase of *Scirpus olneyi* biomass in the elevated chambers in the mixed community coincided with a reduction of *Spartina patens* biomass after four years of exposure. *Distichlis spicata* showed a positive response to elevated CO₂ during the first three years of exposure. No negative effect of elevated CO₂ was found on the pure *Spartina* community, suggesting that the reduction of *Spartina patens* in the mixed community may be due to shading as a result of an increase in biomass of *Scirpus olneyi*.

Scirpus olneyi favors the lower elevations of the marsh (Fig. 7). Density and shoot height are reduced at the higher elevations of the marsh, which may be the result of increased salt or drought stress. *Spartina patens*, which is more salt tolerant, is most abundant at the higher elevations. Growth of *Spartina* may be affected by the higher frequency of flooding and by the low light levels

in the pure *Scirpus* community at the lower elevations. In a high CO₂ environment growth of *Scirpus olneyi* may be expected to expand at the higher elevations of the marsh, at the expense of the C₄ grasses.

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