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Growth and senescence in plant communities exposed to elevated CO_2 concentrations on an estuarine marsh

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Summary. Three high marsh communities on the Chesapeake Bay were exposed to a doubling in ambient CO_2 concentration for one growing season. Open-top chambers were used to raise CO_2 concentrations ca. 340 ppm above ambient over monospecific communities of *Scirpus olneyi* (C_3) and *Spartina patens* (C_4), and a mixed community of *S. olneyi*, *S. patens*, and *Distichlis spicata* (C_4). Plant growth and senescence were monitored by serial, nondestructive censuses. Elevated CO_2 resulted in increased shoot densities and delayed senescence in the C_3 species. This resulted in an increase in primary productivity in *S. olneyi* growing in both the pure and mixed communities. There was no effect of CO_2 on growth in the C_4 species. These results demonstrate that elevated atmospheric CO_2 can cause increased aboveground production in a mature, unmanaged ecosystem.

Key words: Elevated CO_2 – Productivity – Salt marsh – *Scirpus olneyi* – *Spartina patens*

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

Results from studies of agricultural species and, to a lesser degree, wild species have led to several general hypotheses regarding ecological responses to elevated CO_2. Plants with the C_3 pathway of photosynthesis usually increase carbon assimilation and growth in response to increases in CO_2 concentration (Ford and Thorne 1967; Rogers et al. 1983; Downton et al. 1987) whereas C_4 plants

are more variable and generally respond less than C_3 plants (Carlson and Bazzaz 1980; Potvin and Strain 1985; Smith et al. 1987). In communities containing C_3 species, net primary productivity should therefore increase, and C_3 species may gain a competitive advantage over C_4 species (Carter and Peterson 1983; Zangerl and Bazzaz 1984). Both C_3 and C_4 plants show an increase in water use efficiency under elevated CO_2 (Morison 1985). This could have a significant effect on water availability in arid and mesic environments (Wigley and Jones 1985). Low nutrient availability tends to decrease the relative response to CO_2, but the opposite is true for water stress. In environments where plant growth is strongly controlled by one of these limiting factors (e.g. coniferous forests, deserts), the magnitude of the response should vary accordingly (Oechel and Strain 1985).

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

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

Materials and methods

Description of the study site

The study site is located at 38°53′N, 76°33′W in the Rhode River, a subestuary of the Chesapeake Bay. It is typical of brackish high marshes in the Mid-Atlantic region of North America (Whigham et al. 1983). The marsh is infre-

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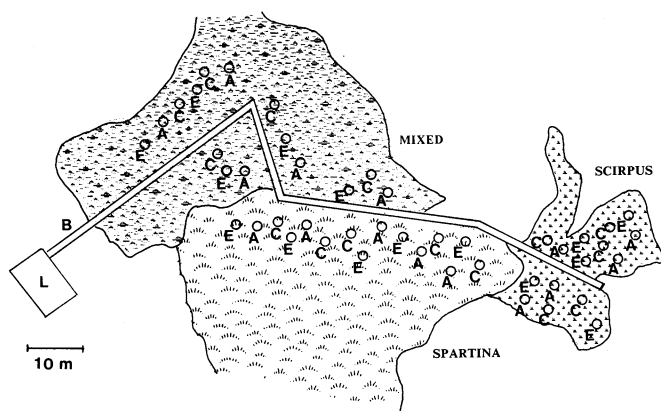
Fig. 1. Map of the study site showing the Scirpus, Spartina and Mixed communities, the field laboratory (*L*), boardwalk (*B*), and permanent experimental plots (*open circles*). The treatments were Elevated chamber (*E*), Ambient chamber (*A*) and unchambered Control (*C*)

quently flooded (Jordan et al. 1983) and is a mosaic of plant associations that are primarily dominated by *Spartina patens* (Ait.) Muhl., *Scirpus olneyi* Grey, *Distichlis spicata* (L.) Greene, *Typha angustifolia* L. or *Iva fructescens* L. Other common species are *Spartina cynosuroides* (L.) Roth, *Scirpus robustus* Pursh, *Hibiscus moscheutos* L. and *Panicum virgatum* L. Three communities on the marsh were selected for this study. One (Spartina) was dominated by the C_4 grass *S. patens*, one (Scirpus) by the C_3 sedge *S. olneyi*, and one (Mixed) by *S. patens, S. olneyi,* and *D. spicata*, also a C_4 grass.

Fifteen permanent circular plots 0.8 m in diameter were established along transect lines in each community (Fig. 1). A 20 cm deep cut was made into the substrate around the perimeter of each plot, severing all living rhizomes. Plastic garden edging was inserted 10 cm into this cut. Treatments within each community (described below) were assigned to plots according to a randomized block design. A preliminary survey of all plots was conducted in late June of 1986 prior to the start of the CO_2 treatment. There were no significant differences in shoot densities among plots assigned to the three treatments in each community.

CO₂ treatment

Open top chambers were used to elevate CO_2 within a plot. The chambers, and the CO_2 control and monitoring system have been described in detail previously (Drake et al. 1987). The chambers were 1.2 m in height and 0.8 m in diameter, were covered with 300 µm polyester film, and were sealed to the marsh surface by taping them to the plastic garden edging. Ambient air was introduced into the chambers by a high capacity blower and circulated with a second blower. In plots exposed to elevated CO_2, 100% CO_2 was continuously injected into the input blower where it was thoroughly mixed with ambient air before entering the chamber. CO_2 levels were measured by an infra-red gas analyser (Binos 4B.2, Leybold-Heraeus, Hanau FRG) connected to an automatic gas sampling system. Light and temperature were monitored both inside and outside chambers at canopy height.

Within each community, five plots were maintained with elevated CO_2 concentrations (Elevated treatment), and five with chambers but exposed to ambient CO_2 concentrations (Ambient treatment). Five plots in each community had no chambers but were otherwise treated identically to chambered plots (Control treatment). CO_2 concentrations inside elevated chambers were allowed to vary diurnally in parallel with ambient variations in CO_2 concentrations. Chambers were placed on the marsh and treatments begun on April 23, 1987 and all chambers were removed from the marsh on November 15, 1987.

Daily mean CO_2 concentrations (sunrise to sunset) were 350 ± 22 (s.d.) $\mu l \, l^{-1}$ inside Ambient chambers and $686 \pm 30 \, \mu l \, l^{-1}$ inside Elevated chambers. Twenty four hour mean temperatures were $1.7 \pm 0.6°$ C higher inside Ambient chambers and $2.0 \pm 0.4°$ C higher inside Elevated chambers than temperatures outside chambers. Light intensity was reduced about 10% inside chambers but light quality was not affected (Drake et al. 1987).

Vegetation sampling

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

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

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

Spartina and Distichlis. Because of the high density of *Spartina* and *Distichlis* shoots, shoot number, biomass, and leaf area were estimated by subsampling each plot. Each plot in the Spartina and Mixed communities was divided into permanent 100 cm² quadrats using monofilament nylon line. Five quadrats per plot were randomly selected for subsampling at the beginning of the season. Combined, these

five quadrats represented 10% of the total plot area. All shoots were counted within each quadrat at each census.

Shoot density per plot was estimated by extrapolation from the mean density in the 5 quadrats. Shoot biomass and leaf area were estimated from limited destructive harvests in each plot at each census. All living shoots within three 25 cm² areas located 2 cm from quadrats in each plot were harvested. Typically, 25–40 stems were collected per plot per census. Senescent material was measured separately from green tissue and no area within a plot was harvested more than once during the season. Leaf area was measured with an electronic leaf area meter. Mean dry weight per shoot was multiplied by shoot density to estimate aboveground biomass per plot.

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

Plant growth analysis

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

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

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

Statistical analysis

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

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

Results

Shoot density

Shoots density of Scirpus was higher in plots with elevated CO_2 in both Scirpus and Mixed communities (Fig. 2A, B). In both cases the effects of CO_2 first became significant at peak density in August and extended through the end
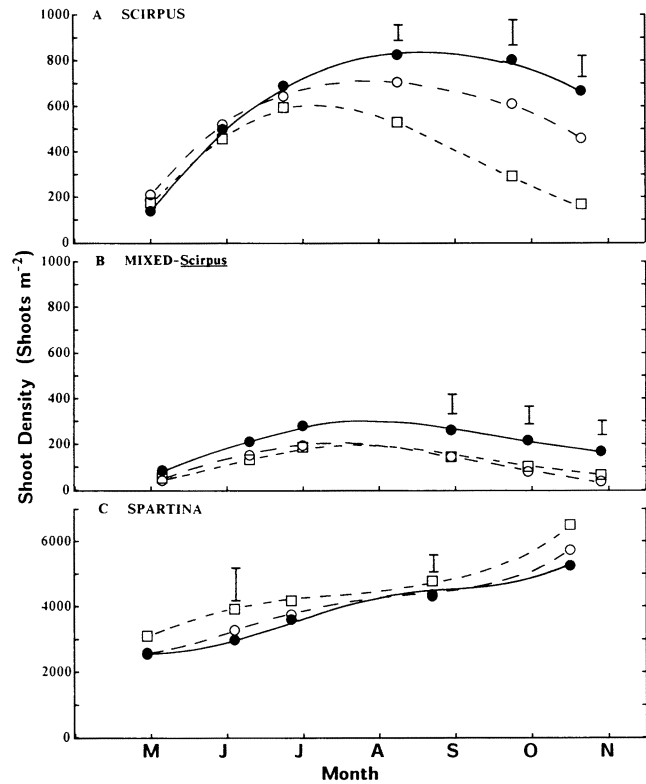

Fig. 2 A–C. The change in shoot density in Scirpus (**A**), Mixed-Scirpus (**B**), and Spartina (**C**) plots. Treatments were Elevated (●), Ambient (○), and Control (□). Vertical bars are the LSD ($P < 0.05$) and are included where significant differences occur (**A** and **B**) or at the second and fourth censuses to indicate variability (**C**)

of the season. There was also a significant difference between shoot densities of Scirpus from Ambient and Control plots in the Scirpus community (Fig. 2A). This chamber effect was not, however, found in the Mixed community (Fig. 2B).

The relative rate of change in shoot density (Shoot Density RGR) was consistently higher in Scirpus community Elevated plots than Ambient plots but this difference was only significant in July, immediately preceeding peak densities (Fig. 3A). In the Mixed community, the effect of CO_2 on Scirpus Shoot Density RGR was seen later in the season, with significant differences between Elevated and Ambient plots in August and September (Fig. 3B). These results indicate both a greater relative allocation of carbon into new shoots and a slower senescence of existing shoots under elevated CO_2.

Shoot densities showed a much more gradual increase over time in the Spartina community (Fig. 2C). Shoot emergence occurred slightly earlier than in Scirpus, with a large number of shoots appearing in mid to late April. There were no significant differences in shoot densities or Shoot Density RGR (data not shown) among Elevated, Ambient, or Control plots at any time.

Shoot weight

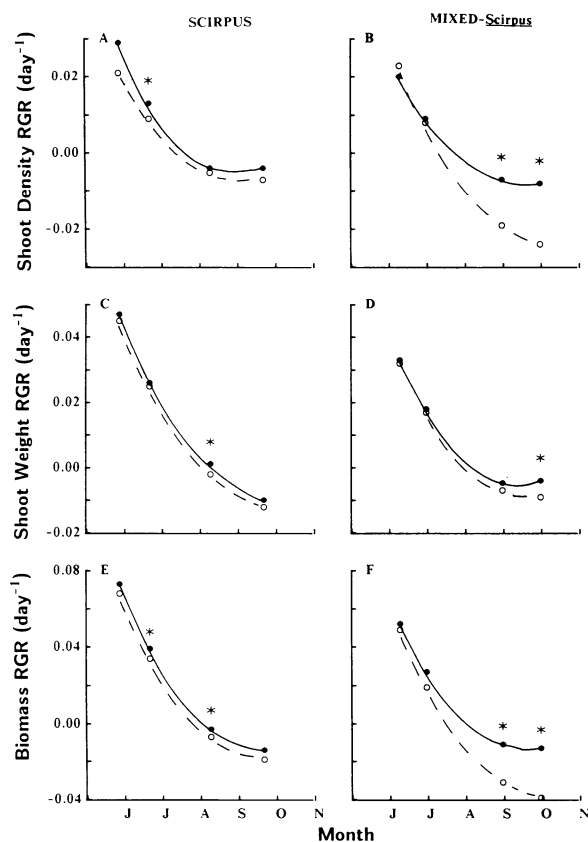CO_2 had no effect on mean shoot weight in the Scirpus community (Fig. 4A). Shoots of Scirpus in the Mixed com-

Fig. 3A–F. Relative change in Shoot Density, Shoot Weight, and Aboveground Biomass from Scirpus (A, C, E) and Mixed-*Scirpus* (B, D, F) plots exposed to Elevated (●) or Ambient (o) CO_2 treatments. Asterixes denote a significant difference ($P < 0.05$) between RGR means within a census

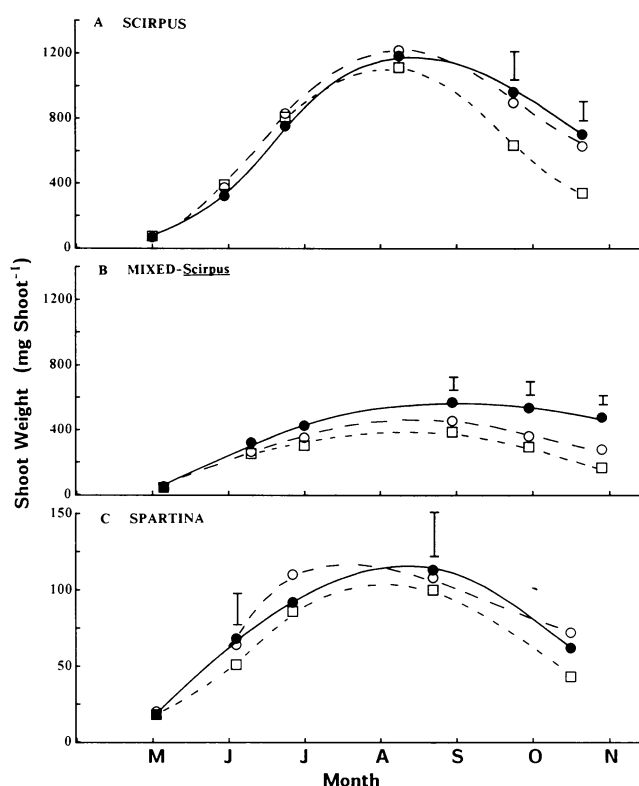
Fig. 4A–C. The change in shoot weight with time in Scirpus (A), Mixed-*Scirpus* (B), and Spartina (C) plots. Treatments were Elevated (●), Ambient (o), and Control (□). Vertical bars are the LSD ($P < 0.05$) and are included where significant differences occur (A and B) or at the second and fourth censuses to indicate variability (C)

munity were less than 50% of the size of shoots in the Scirpus community and there was a significant increase in shoot weight due to CO_2 beginning in late August and extending through the end of the season (Fig. 4B). There was a significant effect of CO_2 on Shoot Weight RGR in the Scirpus and Mixed communities in late August and September (Fig. 3C, D). This response was particularly evident in the Mixed community where shoot weight declined very little through November. There was a significant chamber effect on shoot weight in the Scirpus community in September and October and in the Mixed community in late October (Fig. 4A, B). There were no CO_2 effects on shoot weight in *Spartina* (Fig. 4C). There were also no effects of CO_2 or chamber on SLW from any of the study species (Table 1).

Aboveground biomass

Aboveground live biomass in the Scirpus community increased rapidly between shoot emergence in late-April and the end of July, reaching a maximum of between 600 and 900 g/m² in early August (Fig. 5A). Biomass was significantly higher in Elevated plots in September and October. Peak standing biomass in *Scirpus* from the Mixed community was less than 20% of that from the Scirpus community and there was also a significant response to elevated CO_2 (Fig. 5B). As with shoot density there was a significant

Table 1. Specific leaf weights at peak standing biomass from Elevated, Ambient, and Control plots in three marsh communities. Mean ± (s.e.)

Community	Elevated	Ambient g/cm²	Control
Scirpus	0.0274 (0.0016)	0.0260 (0.0008)	0.0274 (0.0004)
Mixed-*Scirpus*	0.0288 (0.0013)	0.0268 (0.0013)	0.0251 (0.0019)
Spartina	0.0233 (0.0036)	0.0198 (0.0003)	0.0217 (0.0006)
Mixed-*Spartina*	0.0198 (0.0010)	0.0210 (0.0005)	0.0204 (0.0004)
Mixed-*Distichlis*	0.0141 (0.0011)	0.0142 (0.0005)	0.0147 (0.0006)

chamber effect on aboveground biomass only in the Scirpus community.

Although elevated CO_2 had no significant effect on aboveground biomass in the Scirpus community until September, there were small but significant increases in Biomass RGR due to CO_2 in both July and August (Fig. 3E). *Scirpus* in the Mixed community showed similar, although non-significant, differences in Biomass RGR at these times and much greater differences during September and October (Fig. 3F). The CO_2 effects on aboveground biomass were therefore due in part to an increase in the efficiency of new growth (principally through new shoot production)
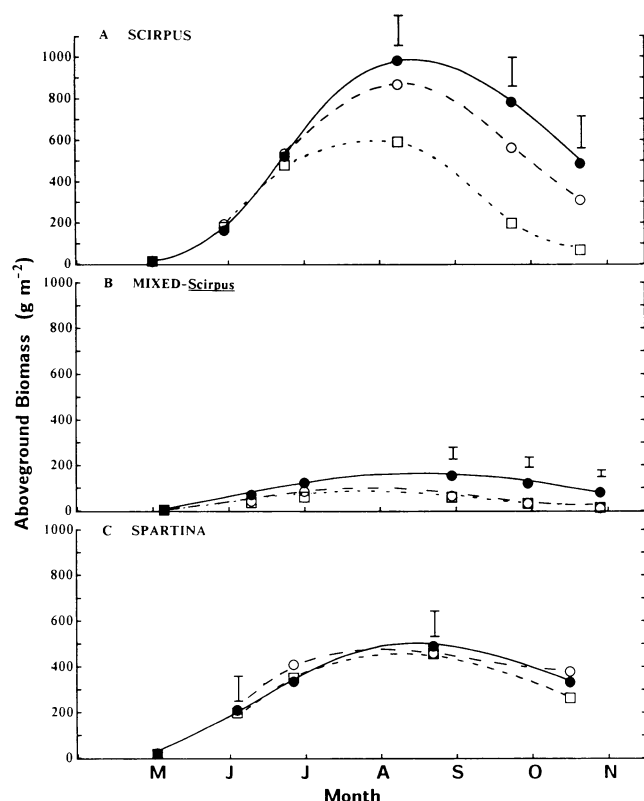
Fig. 5 A–C. The change in aboveground biomass with time in Scirpus (A), Mixed-*Scirpus* (B), and Spartina and Mixed-C_4 (C) plots. Treatments were Elevated (●), Ambient (o), and Control (□). Vertical bars are the LSD ($P<0.05$) and are included where significant differences occur (A and B) or at the second and fourth censuses to indicate variablity (C)

Table 2. Percentage of total biomass (live + senescent) which was senescent at the final census in November 1987 in Elevated, Ambient, and Control plots in three marsh communities. Mean ± (s.e.)

Community	Elevated	Ambient %	Control
Scirpus	35.5 (4.6)[a] *	45.7 (5.6)[b]	79.3 (6.1)[c]
Mixed-*Scirpus*	37.8 (4.6)[a]	80.1 (2.4)[b]	68.7 (6.3)[b]
Spartina	45.3 (4.1)[a]	44.9 (6.0)[a]	53.1 (6.5)[a]
Mixed-*Spartina*	51.8 (9.0)[a]	56.3 (6.6)[a]	69.6 (9.6)[a]
Mixed-*Distichlis*	66.7 (9.3)[a]	64.3 (12.7)[a]	57.2 (11.3)[a]

* similar superscript denotes no significant difference within a community, P<0.05, except Scirpus Elevated vs Ambient where $P<0.10$

and in part to a delay in the loss of dry weight through senescence.

There were no treatment effects on aboveground biomass in *Spartina* (Fig. 5C). Shoot emergence began in mid April and peak biomass of about 500 g/m² was reached in late August. Peak aboveground biomass in the C_4 component of the Mixed community also showed no effect of CO_2 and was very similar (479 ± 27 g m^{-2}, pooled across treatments) to the Spartina community. Analysis of Dry Weight RGR also showed no treatment effects or consistent trends in either community (data not shown).

Table 3. Net primary productivity from Elevated, Ambient, and Control plots in three marsh communities. Mean ± (s.e.)

Community	Elevated	Ambient g/m²	Control
Scirpus	539 (47)[a]	463 (44)[b]	345 (21)[c]
Mixed-*Scirpus*	139 (25)[a]	78 (15)[b]	63 (11)[b]
Spartina	645 (22)[a]	668 (61)[a]	650 (58)[a]
Mixed-C_4	732 (49)[a]	694 (47)[a]	660 (74)[a]

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

The percentage of total *Scirpus* biomass present as dead tissue at the final census in November was significantly lower under elevated CO_2 in both the Scirpus and Mixed communities (Table 2). Again, there was a significant chamber effect in the Scirpus but not the Mixed community. Senescence of the two C_4 species appears to have progressed somewhat more rapidly in the Mixed than in the Spartina community but there was no effect of CO_2 in either case.

Elevated CO_2 caused a significant increase in net primary productivity (NPP) in *Scirpus* from both the Scirpus and Mixed communities (Table 3). Although peak live biomass in the Scirpus community was not significantly higher in Elevated plots, sustained growth later in the season led to greater NPP under elevated CO_2. Senescent *Scirpus* shoots weighed less per cm than did living shoots which resulted in lower NPP than peak aboveground live biomass (Fig. 5A, 5B). Net primary productivity in the C_4 species was greater than in *Scirpus* but was unaffected by elevated CO_2.

Discussion

The most pronounced effect of the doubling in ambient CO_2 concentration on these salt marsh communities was an increase in shoot numbers (Fig. 2) and decrease in the rate of senescence in the C_3 sedge, *Scirpus olneyi* (Fig. 3, Table 3). This resulted in a significant increase in live, aboveground biomass in the latter half of the season (Fig. 5) and greater net primary productivity (Table 4) in *Scirpus* from both the Scirpus and Mixed communities. These results support the prediction that plant growth in mature, unmanaged ecosystems containing C_3 species will increase in response to increasing atmospheric CO_2 concentrations (Bazzaz et al. 1985). We found no growth response in the Spartina community or the C_4 component of the Mixed community.

Our estimates of net primary productivity were based solely on aboveground dry matter and therefore do not take into account the substantial amounts of carbon translocated belowground in perennial marsh species (Good et al. 1982). An increase in carbon allocation to roots or belowground storage organs is a commonly observed response to elevated CO_2 (Ford and Thorne 1967; Bhattacharya et al. 1985). Since shoot number and size early in the season were largely a function of previously stored carbon in *Scirpus americanus* (Giroux and Bedard 1987), a steadily increasing growth response in subsequent years with continuing exposure to elevated CO_2 may be likely in *Scirpus olneyi*. This was not observed, however, in the

arctic sedge *Eriophorum vaginatum* where photosynthetic acclimation to elevated CO_2 occurred within a single season (Tissue and Oechel 1987). Productivity in the arctic tundra is low and growth is strongly nutrient limited (Shaver et al. 1986). The highly productive brackish marsh may be more analogous to C_3 agricultural ecosystems in which growth almost always increases in response to elevated CO_2 (Kimball 1983).

Scirpus shoots arise from axillary buds on the below-ground stem, or rhizome, and are morphologically analogous to tillers in grasses (Esau 1977). An increase in tillering in response to elevated CO_2 has been observed previously in wheat (Gifford 1977; Sionit et al. 1981), the sedge *Eriophorum vaginatum* (Tissue and Oechel 1987) and the C_4 grass *Andropogon glomeratus* (Bowman and Strain 1987). Increased tillering may be a general response to increasing carbon or nutrient supply in monocots producing axillary buds (Fletcher and Dale 1974). In clonal salt marsh grasses, the rate of rhizome and tiller growth is an important factor determining the outcome of competition for open space following disturbance (Bertness and Ellison 1987). The increased shoot growth by *Scirpus* in the Mixed community did not have any detectible negative effect on *Spartina* and *Distichlis* but the long term consequences of a sustained growth response by *Scirpus* in this community are difficult to predict. Regions of the marsh with vigorous *Scirpus* populations have very little *Spartina* or *Distichlis* present. Competition as well as edaphic conditions are probably important in determining local species abundances (Snow and Vince 1984).

The slower rate of senescence and continued production of new shoots in *Scirpus* under elevated CO_2 resulted in a greater number of green shoots present in September and October (Fig. 2), a slower relative rats of decline in above-ground biomass (Fig. 3), and a lower percentage senescent tissue present in November (Table 3). Previous studies of elevated CO_2 effects on whole plant senescence have produced conflicting results. Bhattacharya et al. (1985) found early leaf senescence in sweet potato grown at 675 ppm CO_2 and St. Omer and Horvath (1983) reported early senescence in two California annuals at 2100 ppm but not 700 ppm CO_2. Carter and Peterson (1983) observed delayed senescence in *Sorghum* at 600 ppm CO_2. The mechanism by which CO_2 might affect senescence is not clear. High levels (> 2000 ppm) inhibit the action of ethylene, a senescence promoting hormone (Nooden 1980). Early senescence under elevated CO_2 may be correlated with the timing of other phenological events such as flowering (St. Omer and Horvath 1983) or tuber maturation (Bhattacharya et al. 1985).

The chambers had a significant effect on growth in the Scirpus community although there was no effect on *Scirpus* from the Mixed community or on the C_4 species (Figs. 2, 5). The 2° C temperature increase, protection of shoots from mechanical damage, and possibly higher humidity inside chambers could have contributed to the observed effects on growth. In a review of the literature on plant growth in open top chambers, Drake et al. (1985) found no consistent pattern, with both positive and negative effects reported. They concluded that open top chambers were the best available technology for field exposure of plants to elevated CO_2.

This is the first demonstration that elevated atmospheric CO_2 can lead to an increase in growth and productivity

in an unmanaged ecosystem within a single year. The potential impact of this response on net carbon storage will depend both on the degree to which this response is sustained and the effects of elevated CO_2 on ecosystem carbon loss. With no change or a decline in decomposition rate, an increase in primary productivity could result in greater rates of carbon accretion. This suggests that the direct effects of elevated CO_2 on terrestrial vegetation could be an important consideration in the global carbon budget.

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