Climate impacts on pioneer saltmarsh plants

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ABSTRACT: The 2 grass species that dominate the lower zones of North European saltmarshes utilise different photosynthetic pathways. *Puccinellia maritima*, a C_3 species, occurs at higher elevations than *Spartina anglica*, a C_4 species, which is a relatively recent invader and appears not to form extensive swards in latitudes north of ~54° N because of the limiting effect of low early-season temperatures and the greater competitive ability of *Puccinellia*. We investigate the differential responses of the 2 grasses to rising temperatures and CO_2 concentrations in the light of earlier work that predicts increases in their primary production, assuming a 3°C rise in temperature and a doubling of atmospheric CO_2. Predictions of their responses to climate change are made using evidence from present day competitive interactions in relation to marsh elevation and latitude, and from a competition experiment in which the 2 species were grown under ambient and elevated temperature (+3°C) and ambient and enriched CO_2 (+340 ppm) in all factorial combinations. *Puccinellia* biomass was significantly increased, as expected, by CO_2 enrichment and, probably from increasing early-season growth, by elevated temperature; the effect appeared additive, with the highest yield at the +3°C +340 ppm treatment. *Spartina* growth increased as predicted in response to elevated temperature, but also unexpectedly in high CO_2 treatment, possibly through increased efficiency in water-use. Competition was largely asymmetric in favour of *Puccinellia*, affecting *Spartina* height and shoot weight, with intraspecific effects on tiller production and total biomass; *Spartina* mainly responded to both treatments and competition by increased below-ground growth. These results are compared with other, single-factor, experiments and suggest that, depending critically on some other aspects of climate change such as rising relative sea level and nutrient dynamics, *Spartina* is likely to extend its range northwards as CO_2 and temperatures rise, but *Puccinellia* will continue to replace it in the succession, and probably at lower marsh elevations than at present.

KEY WORDS: *Spartina anglica* · *Puccinellia maritima* · C_4 and C_3 photosynthesis · Elevational niche · Competition · Elevated temperature and CO_2 enrichment · Saltmarsh range extension

1. INTRODUCTION

The seaward edges of European temperate-zone saltmarshes are typically dominated by 2 widespread grass species, *Puccinellia maritima* (Huds.) Parl. and *Spartina anglica* C.E. Hubbard. Although annual plants of *Salicornia* and *Suaeda* species are common as pioneers, these 2 perennial grasses are the effective architects of saltmarsh development—their presence enhancing accretion and saltmarsh growth principally by preventing the resuspension of sediment delivered by the tides to the marsh (Gray et al. 1997, Brown 1998).

They can therefore be described as 'keystone' species, which bioengineer vast tracts of intertidal saltmarsh and have an important rôle in sea defences.

Puccinellia maritima (hereafter simply *Puccinellia*) is widespread in Europe, occurring to 70° N in Norway, and is also found on the southern coast of Greenland and in North America, where it may have been introduced (Gray & Scott 1977). It is frequently the dominant plant over large areas of low and middle saltmarshes, especially those that are grazed or have had a history of grazing. Whereas the first record of *Puccinellia* in the British Isles was in 1655 (Gray & Scott 1977), *Spartina anglica* (hereafter *Spartina*) is by contrast known to have evolved around 1890 following

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hybridisation between the European *S. maritima* and the accidentally-introduced North American species *S. alterniflora*. The origin of this species on the English south coast and its subsequent spread around the world have been remarkably well documented (e.g. Lambert 1964, Marchant 1967, 1968, Ranwell 1967, Gray et al. 1991, Raybould et al. 1991a,b). An aggressive invader, it has come to occupy almost 25% of the saltmarsh in Britain (10 000 ha of the 44 000 ha surveyed by Charman 1990), and occurs in suitable habitats around the coast of Europe from 48 to 57.5° N.

From the viewpoint of this paper, the most important contrast between the 2 species is that they utilise different photosynthetic pathways. *Spartina* is a C_4 species, in which the first product of photosynthetic CO_2 fixation is oxaloacetate instead of phosphoglycerate, as in C_3 species. It is 1 of only 8 known C_4 species in the UK, C_4 photosynthesis being most common in semi-arid tropical and subtropical species, and is only partially adapted to cooler climates (Long 1983). Field studies have shown that significant leaf canopy development does not begin in *Spartina* in south-east England until the mean air temperature exceeds 9°C (Dunn et al. 1981, Long 1983). Thus, low temperatures currently limit the plant's seasonal growth and productivity, and possibly its northward spread. Where water supply is not limiting, photosynthesis in C_4 plants is CO_2-saturated and therefore increases in atmospheric CO_2 are unlikely to increase productivity through increased photosynthesis. However, higher atmospheric CO_2 will increase photosynthesis in C_3 plants such as *Puccinellia*, both under light-limiting and light-saturating conditions, leading to increased productivity (Long 1983, 1990).

When considered in the context of currently predicted scenarios for global climate change, this differential response of *Puccinellia* and *Spartina* to elevated temperatures and atmospheric CO_2, respectively, presents us with fascinating questions. If *Spartina* is able to profit from higher temperatures, particularly in the early spring, could it outcompete *Puccinellia* and other C_3 species, extending its range within individual saltmarshes and estuaries and expanding its geographical range northwards? Equally, might the positive response of *Puccinellia* to CO_2 enrichment allow it to retain a competitive advantage at higher elevations, where it currently replaces *Spartina* in the succession, and to prevent the northward invasion of *Spartina*?

In this paper we address these questions by examining the current interactions between *Puccinellia* and *Spartina* as revealed by their differential distribution in relation to saltmarsh elevation and latitude, we briefly describe a model by Long (1990) that predicts the impact of elevated temperature and CO_2 on the 2 species separately, and we report the results of an experiment in which we have grown them in competition under conditions of both ambient and elevated temperature and CO_2. Finally, we discuss the implications of these findings for future saltmarsh development.

2. INTERACTIONS BETWEEN *PUCCINELLIA* AND *SPARTINA*

2.1. Elevational niches and competition

Although other contributory factors were involved (e.g. vigorous vegetative growth, hybrid origin, extensive planting for mudflat stabilisation), the major reason for *Spartina*'s successful invasion of large areas this century appears to be its ability to occupy mudflats to seaward of, and at lower elevations than, the previous lowest limit of perennial vegetation (usually *Puccinellia*) (Gray 1986, Gray et al. 1995). This has been demonstrated by measuring the upper and lower elevational limits—the elevational 'niche'—of a range of common saltmarsh species (Gray et al. 1991, 1995, Gray 1995). A summary of the results from a survey of 143 transects across saltmarshes in 28 estuaries on the south and west coasts of Britain is given in Fig. 1. The elevational niches of 6 common species are shown along a gradient of standardised marsh heights. The upper and lower limits for each species, on all transects where they are present, were recorded in metres above Ordnance Datum (Newlyn), with absolute height measured from nearby benchmarks, and related to local tidal levels to enable comparisons to be made between transects in terms of their tidal constants. Between 70 and 96% of the variance in the upper and lower limits, depending on the species, could be accounted for by a simple linear relationship
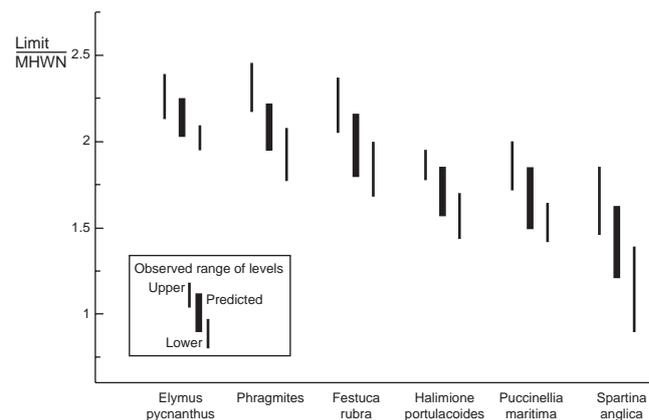

Fig. 1. Elevational ranges and variations in upper and lower limits (m OD) of 6 common saltmarsh plant species along a gradient of standard heights. Predicted range derived from linear regression with Mean High Water Neap tide level

with Mean High Water Neap tide level. For *Puccinellia* and *Spartina* these were:

Puccinellia

Upper limit (m) = 0.12 + 1.80 MHWN (R^2 = 89.5)
Lower limit (m) = 0.23 + 1.39 MHWN (R^2 = 92.3)

Spartina

Upper limit (m) = −0.21 + 1.71 MHWN (R^2 = 96.0)
Lower limit (m) = −0.55 + 1.44 MHWN (R^2 = 95.5)

The elevational niche of *Spartina* clearly extends below that of *Puccinellia* (Fig. 1) by an average of 68 cm, an elevational niche that can include very extensive areas of shallow mudflats.

There is also niche overlap by 20 cm on average. The distribution of the 2 species within this overlap zone is likely to be determined principally by the outcome of interspecific competition. Scholten & Rozema (1990) provided clear evidence of this in a field experiment in which either *Spartina* or *Puccinellia* were removed from subplots within 2 plots set out at slightly different elevations (~4 cm difference, equivalent to 15 to 20 min difference in tidal submergence) in a community where the species were more-or-less homogeneously intermingled. When the regrowth was harvested after 3 mo it was shown that removal of *Puccinellia* caused a significant increase in *Spartina* biomass in the higher plot but not in the lower plot. Conversely, *Spartina* removal caused significant *Puccinellia* biomass increase in the lower but not the higher plot. This pattern of interactions points to the depression of *Spartina* by *Puccinellia* in the higher plot, with the reverse occurring in the lower plot. The outcome of interspecific competition is thus seen to be critically dependent on factors related to marsh elevation.

2.2. Latitudinal variation

The pattern of *Spartina* invasion varies with latitude. In the south of England and the south-west Netherlands, the rapid development of large, monospecific swards earlier this century has in several areas been followed by 'die-back', in which the swards break up and are replaced by mudflats. By contrast, in northern Britain (north of ~54° N) and in the Wadden Sea areas of The Netherlands and Germany, colonising *Spartina* is typically replaced by other species, including *Puccinellia*, at higher elevations. For example, in Morecambe Bay (54° 10′ N) a major expansion began in the 1980s from only 2 clumps in 1968, and more than 100 ha of marsh originally formed by *Spartina* is now a mixed community dominated by *Puccinellia* in which *Spartina* is uncommon (Gray & Rayboult 1997). Although confounded by variation in substrate type, northern marshes being generally more sandy, it has

been suggested that the latitudinal difference in marsh development is related to the effect of temperature on *Spartina* growth (Long et al. 1990, Scholten & Rozema 1990, Gray et al. 1991).

This idea is supported by field measurements of the seasonal growth patterns in *Spartina* and *Puccinellia* in a marsh in east England (52° N). *Puccinellia* increased shoot weight in March, when air temperatures rose above 5°C, with growth peaking in June and July, whereas *Spartina* began to grow in May, when temperatures reached 9°C, and peaked in October (Dunn et al. 1981, Long 1983). Thus, at higher latitudes *Puccinellia* can compete successfully with *Spartina* by earlier annual shoot development.

If the competitive interaction between *Spartina* and *Puccinellia*, or other species which replace *Spartina* as local elevation increases, is affected by temperature, especially spring temperatures, we would predict that the point at which *Spartina* is replaced on a given marsh would be further down the zone of niche overlap with other species the further north the marsh occurs. In fact, an earlier survey of the elevational niche of *Spartina* (Gray et al. 1991, Gray 1992) agrees with that prediction. The regression equation that best described the upper limit of *Spartina* was:

$$\text{Upper limit (m)} = 4.74 + 0.483(R) + 0.068(F) − 0.099(L)$$
$$(R^2 = 90.2, \text{SE} = 0.50)$$

where R = Spring tide range (m), F = fetch in the direction of the transect (km) and L = latitude (decimal °N). Thus, in marshes with a shorter seaward fetch *Spartina* extends further upshore than would be predicted from the effects of tidal range alone, but its upper limit occurs further downshore with increasing latitude.

2.3. Long's predictive model

In 1990, S. P. Long described a simple analytic model for predicting the primary production of *Spartina* and *Puccinellia* under conditions of elevated temperature and CO_2 (Long 1990). The model is based on differences in solar radiation interception and conversion efficiencies, and was validated by comparing the hindcast and observed production for the 2 species on an east England marsh in 1978. The model was then used to predict the changes in the pattern of primary production to be expected in the year 2050, assuming a 3°C rise in temperature and doubling of atmospheric CO_2.

Fig. 2 compares the model output for the 2 yr using daily values of solar radiation interception and conversion efficiency (variables and values given in Table 1 of Long 1990). Increases in annual productivity in 2050 are predicted for both species. Contributory factors
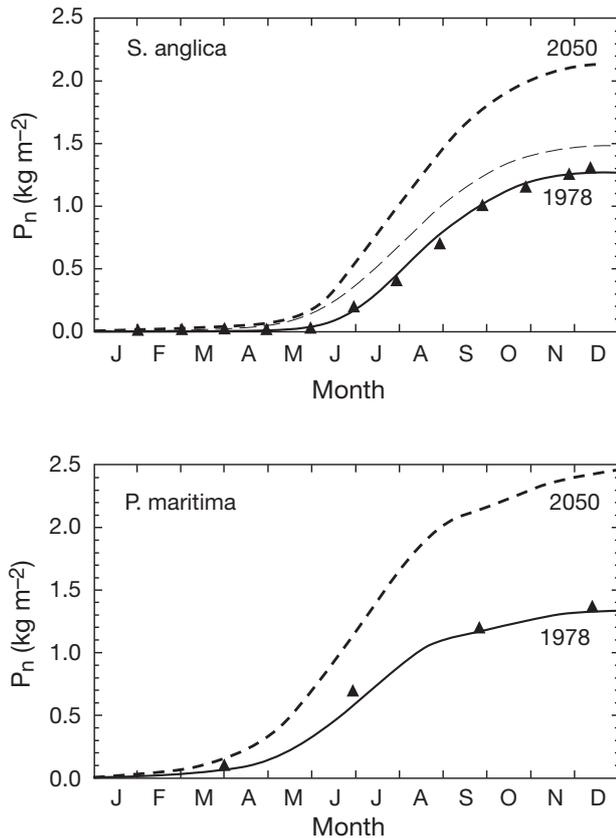
Fig. 2. Cumulative net primary production (P_n) of *Spartina* and *Puccinellia* over 12 mo, predicted from changes in solar radiation and conversion efficiency and assuming a doubling of atmospheric CO_2 in 2050 (from Long 1990). (▲) Net primary production for both species measured on an East Anglian saltmarsh in 1978. For *Spartina*, thin dashed line shows P_n in 1978 if conversion efficiency assumed constant (as in C_3 plants), rather than declining at temperatures <12°C (bold dashed line)

include temperature-driven increases in leaf area, enabling the point where the leaf area index is sufficient to intercept 30% of the incoming radiation to be reached 35 d earlier in *Puccinellia* and 50 d earlier in *Spartina*. This would allow the latter's increased canopy size to capture and utilise high solar radiation input during May and June and, although gaining no direct benefit from higher CO_2 levels, the predicted increase in annual net production is from 1.3 kg m² in 1978 to 2.1 kg m² in 2050. In *Puccinellia* the increase from 1.4 kg m² to 2.5 kg m² in the 2 years is due mainly to higher conversion efficiency in a high CO_2 environment, although the model indicates that *Puccinellia*, too, will gain benefit from increased leaf growth in spring and autumn.

As Long (1990) acknowledges, the model ignores several factors that may change with climate and will affect conversion efficiency and growth. These include the

effects of salinity, nutrient availability and water level changes which may change with rising relative sea levels. In addition, the model, of necessity, does not consider the changes when plants are grown in the presence of neighbours or, in particular, the competitive interactions between the 2 species. An experiment designed to measure these is described in the next section.

3. A COMPETITION EXPERIMENT

3.1. Methods

Plants of *Puccinellia* and *Spartina* were sampled from a saltmarsh at Kents Bank, Morecambe Bay (54° 10′ N), where a relatively recent invasion by *Spartina* has led to the development, through successional displacement, of an extensive *Puccinellia*-dominated saltmarsh. Collected in May 1996, the plants were grown in the south of England in 15 cm diameter pots filled with John Innes No. 2 compost, initially in an unheated glasshouse and after 4 wk in a gravel plunge bed. After 18 wk (October 1996), the growing plants were sampled at random to obtain 160 single-tiller units of each species for the experiment. Tillers were matched for initial size and established in pots of John Innes compost in a replacement series design (de Wit 1960), each series comprising 5 pots each with 4 tillers (4 *Spartina*, 3 *Spartina* + 1 *Puccinellia*, 2 *Spartina* + 2 *Puccinellia*, 1 *Spartina* + 3 *Puccinellia*, and 4 *Puccinellia*). Eight series were set up in 22 cm diameter pots (low density) and 8 in 11 cm diameter pots (high density).

Following establishment for 3 wk, during which dead plants were replaced, the pots were transferred to the solardome facility at the Institute of Terrestrial Ecology, Bangor, North Wales (53° 10′ N). The solardomes (Ashenden et al. 1994) comprise 8 hemispherical glasshouses in which atmospheres are controlled with a high degree of precision to provide 2 levels of temperature (ambient and +3°C tracked continuously above ambient) and 2 CO_2 concentrations (ambient and ambient +340 ppm CO_2). The 8 domes provide 2 replicates for each temperature × CO_2 combination (ambient temperature + ambient CO_2, elevated temperature + ambient CO_2, ambient temperature + elevated CO_2, and elevated temperature and elevated CO_2). A single series of each pot size was placed in each dome and maintained with non-limiting water supplies and a single addition after 20 wk of general-purpose fertiliser (14N : 10P : 27K), before harvesting in September 1997, after 11 mo growth. At harvest, each plant was separated into above- and below-ground material, washed and dry weighed for 2 d at 80°C before scoring for variation in yield. A summary of the results is given below.

Table 1. Individual plant means of 6 yield variables at final harvest in solardome experiment. Treatments (2 domes treatment^{-1}) were: Amb. = ambient temperature, CO_2 tracked to outside; $+°C = +3°C$, ambient CO_2; $+CO_2$ = ambient temperature, 340 ppm CO_2 increase above ambient; ++ = 3°C increase, 340 ppm CO_2 increase. Significance levels from generalised ANOVA, of log transformed values, in which density = effect of pot size (1 df), PPucc = effect of proportion of *Puccinellia* (3 df), CO_2 = effect of elevated CO_2 (1 df), and T = effect of elevated temperature (1 df). Significance *p < 0.05, **p < 0.01, ***p < 0.001. ns, no significant effects detected

Trait	Species	Amb.	+°C	$+CO_2$	++	Significant main effects
Tiller number	*Spartina*	4.10	6.17	6.00	3.48	Density *, $CO_2 \times T$ *
	Puccinellia	31.46	17.69	25.76	25.98	PPucc **, $CO_2 \times T \times$ Density *, $CO_2 \times T \times$ PPucc *
Flowering tillers	*Spartina*	0.13	0.11	0.28	0.01	ns
	Puccinellia	1.79	0.42	1.34	1.53	Density ***, Density $\times$ PPucc *
Plant height (cm)	*Spartina*	15.37	16.69	19.98	17.88	PPucc *
	Puccinellia	44.47	44.08	48.24	54.98	Density ***, $CO_2 \times$ Density *, $CO_2 \times T \times$ Density ***
Shoot weight (g)	*Spartina*	0.45	0.70	0.89	0.37	Density *, PPucc *, $CO_2 \times T$ *, $CO_2 \times T \times$ Density **
	Puccinellia	1.77	1.28	1.61	2.70	Density ***, $CO_2 \times T \times$ Density **
Below-ground weight (g)	*Spartina*	0.61	0.97	1.38	0.60	$CO_2 \times T$ *, $CO_2 \times T \times$ Density **
	Puccinellia	0.42	0.24	0.36	0.37	$CO_2 \times T \times$ PPucc **
Total biomass (g)	*Spartina*	1.04	1.67	1.98	0.97	$CO_2 \times T$ **, $CO_2 \times T \times$ Density **
	Puccinellia	2.19	1.53	1.97	3.08	Density ***, $CO_2 \times T \times$ Density **, $CO_2 \times T \times$ PPucc *

3.2. Results

A general analysis of variance in 6 yield parameters (Table 1) was performed to reveal main effects within the experiment. Those aspects of yield significantly affected by competition were detected by analysing the source of variation due to the proportion of *Puccinellia* in the mixtures, the term 'PPucc' in Table 1. (For *Spartina* this is 0, 25, 50 or 75%, and for *Puccinellia* 100, 75, 50 or 25%.)

The significant effect of density on most variables reflects the importance of differences in the resources available in the different soil volumes and underlines the importance of varying density in such experimental designs (see Section 3.3). However, final yield (biomass) in both species was significantly affected by treatment, either by the interaction between CO_2 level and temperature or the interaction between these treatments and density. The biomass of *Puccinellia* was also affected by the interaction between CO_2 level, temperature and competition. The competition on inspection was seen to be intraspecific, with average yields of 5.30 and 5.19 g in +3°C and enriched CO_2 treatments, respectively, when grown with 3 *Spartina* plants, compared with 1.63 and 2.60 g in those treatments when grown with 3 other *Puccinellia* plants.

In most cases where an interaction effect was detected, *Puccinellia* was the superior competitor, exerting a significant negative effect on the height and above-ground weight of *Spartina*, as well as demonstrating intraspecific competition for tiller number and total biomass. However, the effects on *Puccinellia* root growth appear difficult to interpret. Intraspecific competition is indicated by increasing root weight in pots with fewer *Puccinellia* plants in ambient conditions

(0.37 g in pots with 4 *Puccinellia* to 0.98 g in pots with only 1 *Puccinellia*) and in domes with both elevated temperature and enriched CO_2 (0.29 to 0.72 g). In the treatments with either elevated temperature or enriched CO_2 alone, however, the effect was reversed, with lower mean root weights in *Puccinellia* plants competing with 3 *Spartina* plants than in those growing with 3 other *Puccinellia* plants (0.09 to 0.28 g in +3°C, 0.29 to 0.39 g in enriched CO_2). This indicates interspecific competition, with *Spartina* the superior competitor.

The reason can be seen in the different patterns of response of the 2 species (Fig. 3). *Spartina* responded to both elevated temperature and CO_2 enrichment mainly by an increase in below-ground growth, which includes rhizome production. The significant interaction with density reflects the differences in resources available for growth below ground in the 2 pot sizes. By contrast, *Pucinellia*'s response to higher temperatures and to CO_2 enrichment was mainly to increase the above-ground production. Root growth in *Puccinellia* is affected by CO_2 and temperature but is also restricted by below-ground competition with *Spartina*. These patterns can be seen in both the overall mean values of individual plant biomass (Fig. 3a) and also in the means for plants in pure stands at low density (Fig. 3b). The latter diagram indicates that the relatively poor performance of *Spartina* in the ++ treatment was a real effect and not one resulting solely from competition with *Puccinellia*, which did significantly reduce *Spartina* shoot weight.

The number of flowering tillers, which may be regarded as a measure of potential seed production, was remarkably unaffected by treatment in *Spartina*, and only by density (positively, with significantly more
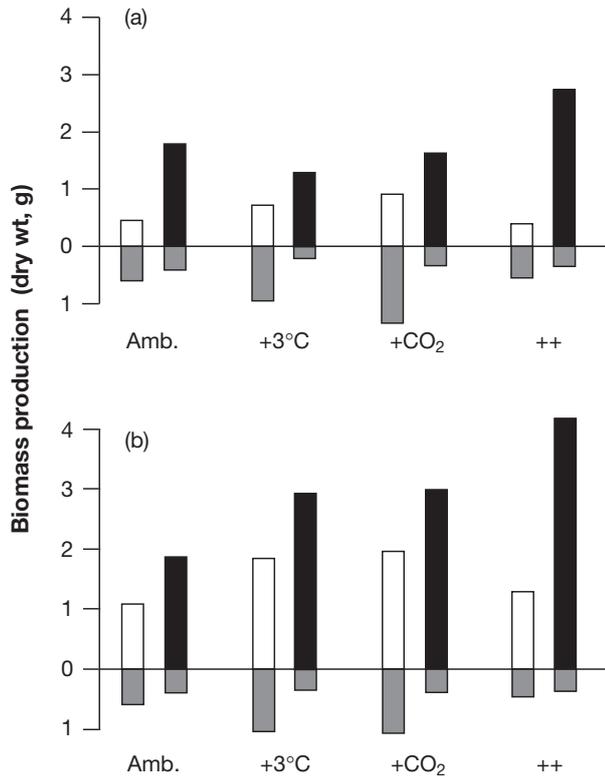
Fig. 3. Biomass production in solardome competition experiment, (a) averaged over all conditions, and (b) in pure stands at low density. Data are mean individual plant biomass at (a) harvest for above-ground material in *Spartina* (open columns) and *Puccinellia* (filled columns) with below-ground biomass (shaded) below the zero line. Treatments (Amb., +3°C, +CO$_2$, ++) as described in text and Table 1

flowering tillers in the smaller pots) and intraspecific competition in *Puccinellia*. Although seed output may be an important aspect of competitive interactions in many species, field evidence (see Section 2.1 above) suggests that vegetative competition is the major force controlling interactions between these 2 perennial grasses.

3.3. Discussion

A comparison of plant growth in ambient conditions with that in elevated temperature plus enriched CO$_2$ provides broad agreement with model predictions (Long 1990) of increased growth. The mean biomass of individual *Puccinellia* plants increased by ~100% in pure stands compared to a predicted increase of ~80% in cumulative net primary production in the model; although these figures are not exactly the same, they are encouragingly similar. Although mean yield increases for *Spartina* in pure stands of 72 and 95% in elevated temperature and CO$_2$ respectively, equate

well with the 62% increase in primary production predicted by the model, the very small increase compared with ambient (5%) in plants grown in pure stands is an unexpected result (Fig. 3b).

The response of *Puccinellia* to enriched CO$_2$ is in line with that found in other empirical studies of C$_3$ species (see review by Bazzaz 1990). Its increased production in elevated temperatures, in pure stands at low density, may reflect the benefit from increased early-season leaf growth, as it would reach the point where it could intercept 30% of the incoming radiation some 35 d earlier (Long 1990). *Spartina*'s response to elevated temperature is also in accordance with predictions and other experiments (Long & Woolhouse 1978, Dunn et al. 1987) but the increased production, particularly below-ground, in enriched CO$_2$ is perhaps surprising, and at variance with earlier work. For example, the C$_4$ grasses *Spartina patens* and *Distichlis spicata* showed no significant response to CO$_2$ enrichment in open top chambers in a Chesapeake Bay salt-marsh, whereas the C$_3$ *Scirpus olneyii* gained significantly more above- and below-ground biomass (Curtis et al. 1989).

It is important, however, to consider not only the effects of competitive interactions, both inter- and intra-specific, but also the interactions between elevated temperature and CO$_2$ and other factors influencing plant growth, including nutrient supply and water relations. For example, Owensby et al. (1993), whose study of a prairie ecosystem also demonstrated that elevated CO$_2$ increased the production of C$_4$ grass species, suggest that increased water-use efficiency associated with partial stomatal closure will be an important mechanism for increasing productivity in natural ecosystems with periodic moisture stress—and will have an impact irrespective of photosynthetic pathway. They concluded that because of this, the C$_4$ perennial tallgrass dominants of these prairies would continue to dominate and, perhaps unless continuous grazing was applied, there would be no shift in competitive advantage in favour of the C$_3$ grasses.

Differences in canopy architecture (Wetzel & van der Valk 1998), the timing of the main phase of competition (Wray & Strain 1987), and the responses induced by varying plant density (Wayne et al. 1999) are among the most important factors influencing the outcome of plant competition. In this study, yield at harvest after 1 yr growth provides a useful snapshot of the interactions of the 2 species, demonstrating the trends in relation to treatment discussed above, and suggesting that competition is mediated by plant height and rhizome development. The generalised ANOVA provides a rigorous test of treatment effects (with only 1 df) and competition (with 3 df) pooling all plants according to treatment. It reveals also the importance of density

and, with the careful initial matching of plant size, thus avoids most of the weaknesses of replacement series designs (Law & Watkinson 1987, Snaydon 1991, Gibson et al. 1999). However, the experiment has limitations due to its size and the fact that only a final harvest was possible, missing the dynamics of the species' interactions. These should be borne in mind when extrapolating to future climate change scenarios.

4. CONCLUSIONS

Bazzaz (1990) and, more recently, Dukes & Mooney (1999) point out that it is risky to make predictions about the impact of climate change on plant species, particularly on the basis of their photosynthetic pathway or their response to CO_2, in the absence of other species. Individual species' responses may be highly modified by the communities to which they belong and by changes in resource levels, the activities of herbivores and pathogens, and a complex of other interactions. Despite this, we believe that the pioneer saltmarsh system presents us with one of the best chances of making a broadly accurate prediction. It is relatively simple, being dominated by 2 grass species whose competitive interactions largely occur at the vegetative phase, and one of the species is demonstrably limited by climate. Furthermore, dispersal, about which major assumptions usually have to be made in modelling and predicting climate-driven shifts in species' range, is not a major issue. Both species are widely dispersed by tides and have small colonies in northern estuaries to act as foci for invasive spread. Finally, although studies have separately demonstrated the complexity of ecosystem-level responses to both elevated temperature (Chapin et al. 1995, Harte & Shaw 1995) and enriched CO_2 (Curtis et al. 1989, Owensby et al. 1993), in this simpler system we have been able to assess the impact of both factors separately and in concert.

On a local scale, the outcome of competition between *Spartina* and *Puccinellia* will clearly depend on the balance between increased CO_2 concentration and temperature, and on the rates at which these change. Whilst an average global warming of 1 to 3.5°C over the next century may be predicted as a result of an increase in greenhouse gases, this is likely to vary spatially and is predicted to be higher in northern latitudes in winter (Houghton 1996). In general, we may expect *Spartina* to extend its range northwards from 57° N, in the lowest zones of saltmarsh, as temperatures and CO_2 levels rise. In those parts of its elevational niche where factors related to tidal submergence prevent the establishment and growth of *Puccinellia*, the increased biomass, and especially the increase in below-ground root and rhizome production, should allow *Spartina* to expand northwards wherever suitable sedimentary environments occur. However, we predict that the competitively superior *Puccinellia* will continue to replace it at appropriate elevations. Further, the additive effect of elevated temperature and CO_2 enrichment on *Puccinellia* performance, coupled with the unexpectedly small increase in *Spartina* growth in such conditions, suggests that *Puccinellia* may invade *Spartina* swards at an earlier successional stage in these northern marshes. The increased competitive superiority of *Puccinellia* under the new regime of both higher temperatures and CO_2 enrichment will also enable it to extend its elevational limits further downshore in existing marshes at latitudes below 57° N.

The net outcome of *Spartina*'s enhanced ability to invade northwards, and *Puccinellia*'s ability to replace it earlier in the succession, is likely to be the northward development of saltmarshes with lower elevational limits than at present. The extent of such pioneer zones will depend on local changes in precipitation regimes, about which global circulation models are as yet too general to be helpful, because high rainfall, mainly through its effect on salinity and particularly on Atlantic coasts, empowers a downshore shift in saltmarsh zones (Adam 1990). Whilst also depending on changes in a number of ecosystem processes such as nutrient dynamics, other aspects of climate change that will be of critical importance in determining the spread of saltmarsh are the impact of rising relative sea level and its relationship on a local scale to sediment availability and accretion rate, and changes in storm frequencies and/or wind direction (e.g Hulme & Jenkins 1998). Interestingly, these largely non-biological variables are proving equally difficult to predict in detail.

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