Wetlands Ecology and Management **9:** 457–461, 2001.

Competition between *Salicornia europaea* and *Atriplex prostrata* (Chenopodiaceae) along an experimental salinity gradient

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Key words: Atriplex, competition, de Wit, halophyte, *Salicornia*, salinity

Abstract

Salicornia europaea L. is a halophyte that often occupies the lowest and most saline (>3.5% total salt) areas of salt marshes. *Atriplex prostrata* Boucher is less salt tolerant than *S. europaea* and often grows in a less saline (<2.0% total salts) zone adjacent to *S. europaea*. The purpose of this experiment was to determine the competitive outcome when these two species are grown at different salinities to ascertain the extent salinity and competition affect plant zonation. Plants were grown in a de Wit replacement series at 85, 170, and 340 mM NaCl in half-strength Hoagland's no. 2 nutrient solution for two months. There was a significant effect of salt concentration, competition, and their interaction on biomass production of *S. europaea* plants. However, only salt concentration significantly affected biomass production of *A. prostrata* plants. Results of this experiment confirmed the results of other studies that demonstrated that the more salt tolerant species were less competitive at lower salinities. *Atriplex prostrata* was the better competitor at 85 mM NaCl, whereas *S. europaea* was the better competitor at 340 mM NaCl because growth of *A. prostrata* was inhibited. At 170 mM NaCl, *A. prostrata* biomass production decreased more than *S. europaea* biomass in mixed culture.

Introduction

The occurrence of species in distinct zones along gradual environmental gradients is most probably the product of their physiological requirements and competitive interactions with other species (Goldberg, 1982; Kenkel et al., 1991). Because selection for competitiveness differs with the degree of physicochemical stress and disturbance that occurs in a particular ecosystem, the competitive ability of plant species may vary significantly in different habitats (Grime, 1979). Dunson and Travis (1991) concluded that it is only through the investigation of interactions between biotic and abiotic factors that community structure and distribution of species can be understood. Actual occurrence of species in zonal communities is related to their tolerance limits and their ability to compete at a particular site (Ernst, 1978; Goldberg, 1982; Kotowski et al., 1998).

Zonal communities in salt marshes are characterized by a reduction in species richness as salt or flooding stress increases (Adam, 1990). Although physicochemical factors are certainly a significant filter determining which species can establish and grow along environmental gradients, interspecific competition is another filter affecting the survival and establishment of species and may help explain the presence of sharp boundaries in species distribution along gradual environmental gradients (Goldberg, 1982; Gaudet and Keddy, 1995; Ungar 1998). Annual species in the genera *Suaeda, Salicornia, Atriplex*, and *Spergularia* are often pioneer invaders of salt marshes, but they are replaced in the successional process by more competitive perennial graminoids (Bertness et al., 1992; Valiela and Rietsma, 1995; Allison, 1996).

Earlier investigations indicate that the density of *Atriplex prostrata* had no significant effect on the growth of the less salt tolerant *Hordeum jubatum* L.

and *Echinochloa crus-galli* L., instead salinity was the primary factor inhibiting their growth (Badger and Ungar, 1990; Rahman and Ungar, 1994). In contrast, at low salinities competition from these latter species inhibited the growth of the more salt tolerant *A. prostrata*. Barbour (1978) and Kenkel et al. (1991) proposed that there was an inverse relationship between competitive ability and the salt tolerance of glycophytes and halophytes. Kenkel et al. (1991) suggested that more experimental studies under controlled laboratory conditions are necessary to separate the effects of salinity and competition on plant distribution along a salinity gradients.

Previous research with the two species being investigated has shown that *Salicornia europaea*, a leafless succulent, is more salt tolerant than *Atriplex prostrata*. It can grow in portions of the marsh with salinities greater than 3.5% total salts, while *A. prostrata* usually grows in areas of lower salinity (<2.0% total salts) (Ungar et al., 1979). Due to their different ranges of salt tolerance, these two species are often found growing in different zones in a salt marsh. *Salicornia europaea* is usually found in the most saline areas of the marsh, while *A. prostrata* inhabits adjacent less saline areas of the marsh (McMahon and Ungar, 1978; Riehl and Ungar, 1983).

Although *S. europaea* and *A. prostrata* differ in their level of salt tolerance, the dominance of one of these species over another in a certain salinity zone may be determined by the physiological tolerance limits of each species in hypersaline sites, but their relative competitive abilities may play a significant role in areas of low (<0.5%) or intermediate salinity (1.0 to 2.0% total salts) (Ungar, 1991). Growth of *S. europaea* is stimulated at salinities of 1.0% total salts, but it is often absent at this salinity from field sites that are dominated by *A. prostrata* (Ungar, 1991). Although halophytes are generally considered to be poor competitors when compared to glycophytes, some field studies have reported a competitive interaction among halophytes that may affect the zonation of species (Ungar et al., 1979; Ellison, 1987; Badger and Ungar, 1990; Adam, 1990).

The purpose of the present investigation was to determine how competition affected growth of the salt marsh species *Salicornia europaea* and *Atriplex prostrata* over a range of salinities in a replacement experiment (de Wit, 1960). Although there has been criticism of the replacement series technique, Hamilton (1994) indicated that it is appropriate for experiments questioning the similarity of response to stress (e.g. salt tolerance) of competing taxa.

Materials and methods

Salicornia europaea and *Atriplex prostrata* seedlings were collected on 25 June 1997 in Rittman, Ohio (Wayne County) from a salt marsh on an abandoned well field belonging to the Morton Salt Company. This salt marsh consists of zones with decreasing salinity levels, *S. europaea* (3.5% total salts, 49 mS/cm), *Atriplex prostrata* (1.3% total salts, 20 mS/cm), and *Hordeum jubatum* (< 0.6% total salts, <10 mS/cm) (Ungar et al., 1979). The high, medium, and low salt treatments in our experiment are within the range of salinities found under field conditions. Mean shoot length at time of transplant for *S. europaea* and *A. prostrata* was 8.8 cm and 6.8 cm respectively. Plants were separated from their field soils and grown in fine sand in half strength Hoagland and Arnon no. 2 nutrient solution (Moore, 1960) at 85 mM (0.5%, 8.4 mS/cm) 170 mM (1.0%, 16.7 mS/cm), and 340 mM (2.0%, 33.4 mS/cm), NaCl. *Salicornia europaea* is an obligate halophyte and plants were therefore placed in 170 mM NaCl on 29 June 1997 to prevent wilting. All plants were grown in the following proportions, 8 *Salicornia* (S): 0 *Atriplex* (A), 6 *S*: 2 *A*, 4 *S*: 4 *A*, 2 *S*: 6 *A*, 0 *S*: 8 *A*, in round plastic pots (9 cm dia × 5 cm high) and were watered with 85, 170, and 340 mM NaCl. Nutrient solutions were maintained at a constant level throughout the experiment to maintain consistent salinity concentrations. A replacement series (de Wit, 1960) was employed to determine the effect of one species upon the other when grown in different proportions at a constant density of 8 plants per plot (1,258 plants/m^2). These densities represent values found under field conditions (McGraw and Ungar, 1981; Wertis and Ungar, 1986). Seven replicates were used for each treatment combination (n = 7).

Plants were grown in a growth chamber for 60 days at 25 °C in a long day (15 h) light period (276 μmol photons m^{-2} sec^{-1}, 400–700 nm) and in a 15 °C (9 h) dark period. Pots were randomized weekly after plants were established. Roots and shoots were harvested on 29 August 1997 after 60 days of treatment, placed in a drying oven at 60 °C for 48 hr, and weighed to determine whole plant dry mass. Differences among means were determined with a two-way ANOVA for each species. A Bonferroni post-hoc test was used to

Table 1. Two-way ANOVA for mean biomass per plant of *Salicornia europaea* and *Atriplex prostrata*.

Source	df	Mean squares	F-Ratio	Prob
S. europaea				
Concentration	2	0.0027	4.39	0.016
Competition	3	0.0024	3.86	0.013
Interaction	6	0.0025	4.07	0.001
Error	72	0.0006		
Total	83	0.0090		
A. prostrata				
Concentration	2	0.0153	10.52	<0.001
Competition	3	0.0015	1.05	0.375
Interaction	6	0.0027	1.86	0.100
Error	72	0.0015		
Total	83	0.0018		

Table 2. Mean (± S.E.) dry mass (g/plant) for *Salicornia europaea* and *Atriplex prostrata* grown in a de Wit replacement series. Lowercase letters represent significant differences among all columns, capital letters represent significant differences among rows.

Mean (± S.E.) dry mass (g) per plant for *Salicornia europaea*

	mM NaCl		
	85	170	340
8 Se: 0 Ap	$0.108 \pm 0.009^{b}_{A}$	$0.082 \pm 0.016^{a}_{A}$	$0.081 \pm 0.004^{a}_{A}$
6 Se: 2 Ap	$0.048 \pm 0.008^{a}_{A}$	$0.083 \pm 0.006^{a}_{A}$	$0.076 \pm 0.007^{a}_{A}$
4 Se: 4 Ap	$0.062 \pm 0.010^{ab}_{A}$	$0.050 \pm 0.006^{a}_{A}$	$0.091 \pm 0.007^{a}_{A}$
2 Se: 6 Ap	$0.059 \pm 0.009^{a}_{A}$	$0.060 \pm 0.015^{a}_{A}$	$0.096 \pm 0.015^{a}_{A}$

Mean (± SE) dry mass per plant for *Atriplex prostrata*

	mM NaCl		
	85	170	340
6 Se: 2 Ap	$0.142 \pm 0.042^{a}_{B}$	$0.063 \pm 0.006^{a}_{A}$	$0.058 \pm 0.009^{a}_{A}$
4 Se: 4 Ap	$0.097 \pm 0.004^{a}_{A}$	$0.066 \pm 0.008^{a}_{A}$	$0.054 \pm 0.002^{a}_{A}$
2 Se: 6 Ap	$0.086 \pm 0.007^{a}_{A}$	$0.048 \pm 0.014^{a}_{A}$	$0.069 \pm 0.005^{a}_{A}$
0 Se: 8 Ap	$0.084 \pm 0.005^{a}_{A}$	$0.084 \pm 0.001^{a}_{A}$	$0.056 \pm 0.006^{a}_{A}$

Means with the same superscript letter are not significantly different ($p = 0.05$) from one another using the Bonferroni multiple comparison test. Lower case letters denote differences within a column, uppercase letters denote differences within a row.

determine if differences between individual treatment means were significant (Hintze, 1995).

Results

Dry mass production of *S. europaea* plants was significantly affected by salt concentration, competition, and an interaction between salt concentration and competition (Table 1). A significant interaction occurs because at 340 mM NaCl there is no significant competition effect on dry mass production of *S. europaea*. Conversely, salt concentration was the only factor significantly affecting dry mass production of *A. prostrata* (Table 1).

A Bonferroni multiple comparison test showed that *S. europaea* grown in 85 mM NaCl with a proportion of 8 *Se*: 0 *Ap* had significantly higher dry weight biomass than *S. europaea* grown in the same salt concentrations with ratios of 6 *Se*: 2 *Ap* and 2 *Se*: 6 *Ap*. *Salicornia europaea* grown in a proportion of 4 *Se*: 4 *Ap* were not significantly different from any group grown in 85 mM NaCl (Table 2). Within the 170 mm and 340 mM NaCl treatment groups there were no significant differences in biomass for *S. europaea* among the different proportions of *S. europaea* and *A. prostrata*. When comparing biomass at a given proportion of *S. europaea* to *A. prostrata* among the salt concentrations there were no significant differences in biomass for *S. europaea* (Table 2).

For *A. prostrata* a Bonferroni multiple comparison test demonstrated that there were no significant differences within a salt concentration for dry weight biomass for any of the ratios of *S. europaea* to *A. prostrata*. The Bonferroni test also demonstrated only one significant difference in biomass for a given proportion among salinities. *Atriplex prostrata* grown in a ratio of 6 *Se*: 2 *Ap* had significantly more biomass at 85 mM NaCl than at 340 mM NaCl (Table 2).

At 340 mM NaCl, *S. europaea* and *A. prostrata* grew at approximately their expected levels (based on control values) at most of the different proportions. The expected level is determined graphically by drawing a straight line from the highest proportion to the lowest proportion for each species for relative biomass (represented by a dotted line, Figure 1). When the relative biomass falls below this line then that species is not doing as well as expected and if the biomass is above this line than that species is doing better than expected. One noticeable difference was that the relative biomass of *A. prostrata* was greater than expected from control values at the highest proportion (2 *S*: 6 *A*; Figure 1) in 340 mM NaCl. At 170 mM NaCl, *S. europaea* did not grow as well as expected from control values in the 4 *S*: 4 *A* treatment and at 85 mM NaCl a reduction in growth occurred in all species ratios.

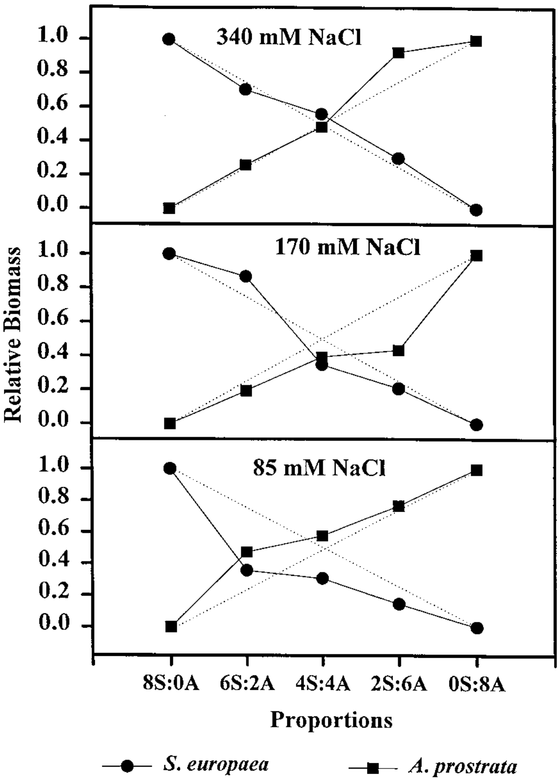

Figure 1. Relative biomass of *Salicornia europaea* and *Atriplex prostrata* grown in a competitive replacement series at 85, 170, and 340 mM NaCl. Solid line represents actual plant growth, whereas dotted line represents expected level of growth for each species based on growth in controls without competition.

Discussion

Ungar (1977) demonstrated a high correlation between soil water potential and leaf water potential, indicating that *A. prostrata* could not survive in a saline environment unless it was able to adjust its water potential to a more negative level than that of the soil solution. It was shown that *S. europaea* was able to adjust its water potential to more than –1.0 MPa below that of *A. prostrata*, indicating that *S. europaea* can grow in more saline areas (Ungar, 1977).

Ungar et al. (1979) determined that shifts in zonal distribution of plant species were correlated with changes in salt concentrations in an inland salt marsh. These de Wit replacement series data are consistent with the results from field competition experiments with *S. europaea* and *A. prostrata*, where it was observed that the distribution of *S. europaea* was related to both competition at low salinities and tolerance to stress at high salinities (Ungar et al., 1979). Soil cores containing *S. europaea* were transplanted along a salinity gradient in cleared and uncleared plots on a salt marsh, and it was demonstrated that when not competing against other species in the *A. prostrata* zone or the less saline *Hordeum jubatum* zone the optimal conditions for *S. europaea* growth was at these lower salinities (< 1.0% total salts). These results agree with our replacement series data, where *S. europaea* had the highest biomass when grown in a monoculture at the lowest salinity, but *S. europaea* biomass was not significantly reduced when the proportion of *S. europaea*: *A. prostrata* decreased from 6: 2 to 2: 6 at the lowest salinity (85 mM NaCl).

Growth responses of *A. prostrata* in our experiment are consistent with the field data of McMahon and Ungar (1978) who found that *A. prostrata* zonation is limited to intermediate salinities (<2.0% total salts) because it cannot tolerate higher salinities. Present results were similar in that *A. prostrata* grown in a ratio of 6 Se: 2 Ap had significantly higher biomass production at 85 mM NaCl than those plants in the 340 mM NaCl treatment. Although positive interactions are reported for species that inhabit salt marshes (Bertness, 1991; Bertness and Hacker, 1994; Bertness and Ming Yeh, 1994), the results of this competition study support the hypothesis that at higher salt concentrations *S. europaea* (the more salt tolerant species) is successful because *A. prostrata* grows poorly at high salinities. Our data suggests that *A. prostrata* may inhibit the spread of *S. europaea* into the lower salinity zone of a salt marsh because of competition, but is limited itself by high salt concentrations in the *S. europaea* zone.

The trend in the present data is supported by a similar study in which three grass species of differing halotolerance were more competitive in different portions of a salinity gradient because they varied in their level of salt tolerance (Kenkel et al., 1991). *Poa pratensis* L. (glycophyte), *Hordeum jubatum* (intermediate salt tolerance), and *Puccinellia nuttalliana* (Schultes) A. Hitchc. (high salt tolerance) were grown in monoculture and mixtures over a gradient of salinities ranging from 0 to 14 g NaCl/L (250 mm). It was determined that all three of these species grew best at 0 g NaCl/L when grown in monoculture. However, when grown in a mixture, *P. pratensis* was the best competitor at low salinities, *H. jubatum* was the best competitor at intermediate salinities, and *P. nuttalliana* was the best competitor at the high salinities (Kenkel et al., 1991). They concluded that there was a reciprocal relationship between the salt tolerance of these grass species and their competitive ability.

Zonation of halophytes is controlled by physicochemical factors (Wilson et al., 1996), but as indicated in this investigation interspecific competition may also play an important role in determining a species distribution in a salt marsh. The present controlled laboratory study supports the results of field studies, demonstrating that zonation in a salt marsh is determined not only by the salt tolerance of a species but also by a species competitive ability at a given salt concentration. Our data are consistent with the hypothesis of Kenkel et al. (1991), indicating that there may be a reciprocal relationship between the salt tolerance of species and their competitive ability.

Acknowledgements

The authors thank Christy T. Carter for her assistance in plant maintenance and J. Forrest Meekins for her editorial comments.

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