

# Competition and the response of three plant species to a salinity gradient<sup>1</sup>

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Three grasses (*Poa pratensis*, *Hordeum jubatum*, and *Puccinellia nuttalliana*) were grown in monoculture and three-species mixture at each of eight salinity levels in a controlled environment chamber. In monoculture, all species grew best when no salts were added to the nutrient medium. When salts were added the species showed differing degrees of salt tolerance. Percent decreases in total biomass with increasing salinity and shifts in aboveground to belowground biomass ratios suggested increased salt tolerance in the order *P. pratensis* < *H. jubatum* < *P. nuttalliana*. In mixture, all species showed a significant change in salinity response when compared with their responses in monoculture. Interspecific competition resulted in *P. pratensis* being suppressed at all but the lowest salinities. *Hordeum jubatum* showed the least suppression at intermediate salinities, while *P. nuttalliana* was least suppressed at the highest salinities. These results indicate that interspecific competition results in a shift in the peak performance of more salt-tolerant species toward the high end of the salinity gradient. The species distributions in our experimental mixtures reflected those observed in the field, suggesting that competition plays an important role in structuring inland saline plant communities.

*Key words*: halophyte, glycophyte, community, *Hordeum jubatum*, *Puccinellia nuttalliana*, *Poa pratensis*.

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Trois plantes herbacées (*Poa pratensis*, *Hordeum jubatum* et *Puccinella nuttalliana*) ont été cultivées en monoculture et en mélanges des trois espèces, en présence de huit teneurs en sel, les expériences étant conduites en chambre de croissance. En monoculture, chacune des espèces a le mieux poussée en absence de sels. Lorsque les sels ont été ajoutés, les espèces ont montré des degrés divers de tolérance aux sels. Les données sur la diminution relative de la biomasse avec l'augmentation de la salinité et le déplacement des ratios des biomasses aériennes et racinaires suggèrent l'existence d'une tolérance croissante dans l'ordre suivant: *P. pratensis* < *H. jubatum* < *P. nuttalliana*. En mélange, toutes les espèces montrent un changement significatif dans leurs réactions à la salinité si on les compare à leurs réactions en monoculture. La compétition interspécifique conduit à la suppression du *P. pratensis* à toutes les concentrations sauf aux plus basses teneurs en sels. *Hordeum jubatum* montre un minimum de suppression aux teneurs intermédiaires en sels, alors que le *P. nuttalliana* est le moins supprimé aux teneurs les plus élevées en sels. Ces résultats montrent que la compétition interspécifique a entraîné un déplacement de l'optimum de croissance relative des espèces les plus tolérantes aux sels vers la partie supérieure du gradient de salinité. Les distributions des espèces observées dans les mélanges expérimentaux sont comparables à celles observées aux champs, ce qui suggère que la compétition joue un rôle important dans le développement des communautés salines terrestres.

*Mots clés* : halophyte, glycophyte, communauté, *Hordeum jubatum*, *Puccinellia nuttalliana*, *Poa pratensis*.

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## Introduction

Vegetation zonation in coastal and inland saline environments of North America has been noted in a number of studies (Ungar 1974a; Haines and Dunn 1985; Bertness and Ellison 1987). Both competition and environmental variation have been suggested as important factors causing zonation in these systems, but few studies have experimentally tested this hypothesis. In coastal marshes, investigations of vegetation–environment relationships suggest that zonation is closely linked to environmental discontinuities resulting from tidal rhythms (see Cooper 1982). In inland saline systems, however, vegetation discontinuities are often not linked to environmental discontinuities (Ungar 1974a). Because descriptive studies cannot generate information on levels of interspecific interaction (Silander and Antonovics 1982), manipulative field and laboratory experiments are required to determine the role that competition plays in creating vegetation zonation; demonstrating a correspondence between vegetation “edges” and environmental discontinuities (e.g., Johnson et al. 1985) does not prove that competition is unimportant.

The role of interspecific competition in organizing and structuring plant communities is typically examined by performing perturbation experiments in the field. In coastal ecosystems, such experiments have indicated that environmental variation, disturbance, and interspecific competition are all important factors in the formation of vegetation zones (Silander and Antonovics 1982; Snow and Vince 1984; Bertness and Ellison 1987). In these studies the role of competition is inferred from results indicating that species normally found at high salinity perform better in less saline areas when not subjected to interspecific competition. This suggests that more salt-tolerant species are excluded from areas of low salinity by competitive exclusion. The principal advantage of such experiments is that they are performed under natural conditions. However, since gradients in the field are environmentally complex, it may be difficult to determine unequivocally which environmental factors are most important in controlling species distributions. Furthermore, because field investigations are time specific (Silander and Antonovics 1982), interpretations may be misleading if based on results from a single growing season.

Controlled laboratory experiments offer a more direct approach to examining competitive interactions in plants. However, most such experiments have concentrated on pair-

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However, most such experiments have concentrated on pairwise interactions and have generally been restricted to a few levels of one (occasionally two) environmental factor. While some authors have expressed the opinion that results of pairwise competition experiments might be successfully extrapolated to predict multispecies interactions (e.g., Harper 1982), others feel that experimental approaches involving competition between many species must be developed (see Austin and Austin 1980). The multispecies experimental approach was pioneered by Ellenberg (1954). He created a water table gradient along which four grass species were sown in monoculture and four-species mixture, in two replicates. Monoculture and mixture responses along the gradient were similar for three of the species, but the response of the fourth changed when grown in mixture. From this and other studies, Ellenberg concluded that interspecific competition is important in determining species distributions under natural conditions (but see Ernst 1978). Later studies using Ellenberg's approach obtained similar results (Mueller-Dombois and Sims 1966; Pickett and Bazazz 1978; Austin and Austin 1980). Unfortunately, replication was not used in these studies, making statistical inference difficult. Austin et al. (1985) used replication but did not directly address the question of whether species responses differed in monoculture and mixture.

The experiment described here follows from a survey of vegetation-environment relationships of NaCl-dominated saline flats in central Manitoba, Canada (Burchill and Kenkel 1991). On these flats, we found that boundaries between vegetation zones did not correspond to environmental discontinuities. This confirmed observations from inland saline areas throughout North America (see Ungar 1974a) and led us to hypothesize that interspecific competition plays a role in organizing vegetation along salinity gradients. We tested this hypothesis using an experimental salinity gradient in a modification of Ellenberg's multispecies approach with replication. Three grasses (*Poa pratensis* L., *Hordeum jubatum* L., and *Puccinellia nuttalliana* (Schultes) A.S. Hitchc.) were grown at eight salinity levels, both in monoculture and three-species mixture. Our objectives were (i) to statistically compare the monoculture and mixture responses of each species along the salinity gradient and (ii) to assess the hypothesis that competition and salinity together play a role in creating vegetation zonation in the field.

## Materials and methods

### Species and germination

The three species chosen for our study are found in or near saline sites, have similar growth forms, and have viable seed that is available in sufficient quantities. Previous studies indicated that *P. nuttalliana* is one of the most salt-tolerant grasses (Macke and Ungar 1971), while *H. jubatum* tolerates intermediate salinities (Ungar 1974b). Seed of these two species was collected in September 1989 from saline flats at the University of Manitoba Field Station, Delta Marsh (50°11'N, 98°23'W). The glycophyte *P. pratensis* (Canada No. 1 Park Variety Bluegrass, T&T Seeds Ltd., Winnipeg, Man.) was chosen as a representative salt-intolerant species. *Hordeum jubatum* and *P. nuttalliana* commonly dominate vegetation zones in saline areas of Manitoba (Burchill and Kenkel 1991), while *P. pratensis* is often found near saline sites.

Germination trials were performed in a controlled environment chamber with a 16-h light - 8-h dark cycle and 25°C-4°C ( $\pm 1.5^\circ\text{C}$ ) temperature cycle. Temperature fluctuation was used since it encourages seed germination in many halophyte species (Ungar 1987). For each species, 100 mg of seed was carefully sprinkled over 500 g (dry

weight) of washed silica sand in 10 cm diameter plastic pots. Seeds were gently pressed into the sand and covered with an additional 10 g of dry sand. Pots were covered with a plastic Petri dish lid to prevent desiccation and were watered from the bottom by placing them in acrylic drain trays filled with distilled water. Salt was not added to the water, as halophyte seeds germinate best under nonsaline conditions (Flowers et al. 1986). Germination results indicated that 42 mg of *P. nuttalliana*, 263 mg of *H. jubatum*, and 294 mg of *P. pratensis* seed were required to obtain 150 seedlings per pot.

### Experimental design

Species were grown in monoculture (150 plants/pot) and three-species mixture (150 plants of each species/pot) at eight salinity levels. There were three replicates of each "treatment" combination for a total of  $4 \times 8 \times 3 = 96$  pots. Initial growing conditions were identical to those described in the germination experiment above, except that the pots were placed in plastic Petri dishes supported by acrylic rods within the drain trays. This prevented salt contamination from occurring between treatment levels. Pot positions were randomized initially and rerandomized three times during the experiment to minimize the effect of environmental differences within the chamber (Potvin et al. 1990).

By day 8 of the experiment, all three species had germinated and Petri dish lids were removed from the tops of pots. On day 12, the night temperature was increased to 10°C and nutrient medium (one-quarter strength modified Hoagland's solution; Behringer 1973) was added to the pots from the bottom by filling the acrylic drain trays. Beginning on day 19, 150 mL of nutrient medium was added to each pot from the top (150 mL was sufficient to completely flush out the old medium). At this stage the medium contained initial levels of 0, 0.75, 1.5, 2.25, 3.0, 3.75, 4.5, and 5.25 g NaCl·L<sup>-1</sup>. Salt levels were gradually increased to final levels of 0, 2, 4, 6, 8, 10, 12, and 14 g NaCl·L<sup>-1</sup> by day 29 of the experiment. Salinity was increased gradually to mimic the trend of increasing salinity that occurs in the field from spring to summer and to minimize osmotic shock to seedlings. The salinity levels used in this experiment were within the range of those observed in the field; mean soil water salinity values over two summers in a Lake Winnipegosis salt pan were 10.5 g salt·L<sup>-1</sup> in the *H. jubatum* zone and 26.6 g salt·L<sup>-1</sup> in the *P. nuttalliana* zone.

To maintain constant salinities and an adequate nutrient supply, pots were flushed with 150 mL of the nutrient-salt medium twice a week for the duration of the experiment. On other days distilled water was carefully added to pots in amounts sufficient to saturate the soil without flushing medium from the pots. Towards the end of the experiment, it was necessary to water plants twice daily to prevent desiccation.

On day 94 aboveground and belowground biomass of monoculture pots was harvested, dried at 85°C, and mass determined to  $\pm 0.01$  g. Aboveground biomass in the mixture pots (separated by species) was determined in the same way. It was not possible to separate the belowground biomass of mixtures by species.

### Data analysis

To assess relative salinity tolerance, we calculated the relative total biomass (RTB) for each species at the eight salinity levels:

$$[1] \quad \text{RTB}_i = \frac{\text{monoculture total biomass at salinity level } i}{\text{mean monoculture total biomass at zero salinity}}$$

Since all three species accumulated the highest total (aboveground + belowground) biomass at zero salinity, this ratio expresses the proportional loss in total biomass at higher salinities. We also computed the aboveground to belowground biomass ratio at each salinity level for each species.

Data for each species were analyzed separately (using aboveground biomass data) to determine whether or not interspecific competition affected species responses to salinity. For this purpose we used an implementation of the general linear model (see Table 1) in which species biomass was a function of both salinity level (*S*) and com-

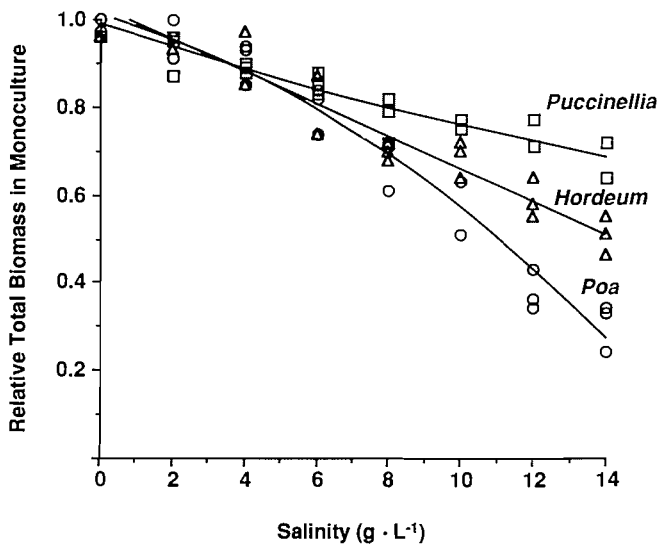


FIG. 1. The effect of salinity on relative total biomass (RTB) for *Poa pratensis*, *Hordeum jubatum*, and *Puccinellia nuttalliana* grown in monoculture. Second-order polynomials are fitted to the data.

petition (C, monoculture versus mixture). Our model can be thought of as a hybrid between the analysis of variance and regression analysis (Freund et al. 1986, pp. 141–157), with a quadratic salinity term ( $S^2$ ) included to account for nonlinear species responses to salinity (Snedecor and Cochran 1967, p. 460). Note that regression is most often used in this way to remove unwanted variation in an analysis of variance under the assumption of no interaction between the regression and treatment terms (Mead 1988, p. 246). In our experiment, however, we specifically focus on the interaction terms  $SC$  and  $S^2C$ , as they indicate whether the quadratic regressions of biomass against salinity differ in slope ( $SC$  significant) and (or) curve shape ( $S^2C$  significant). In other words, the presence of significant interaction implies that species responses to salinity differ between monoculture and mixture. The analyses were performed using the SAS procedure GLM (SAS Institute Inc. 1985). For completeness, results of the general linear model analyses are presented with both sequential (type I) and partial (type III) sums of squares. Residuals were tested for normality using the Shapiro-Wilk  $W$ -statistic and for equality of variances using the Bartlett test (Neter and Wasserman 1974).

A summary of the responses of the three species in mixture was obtained by relativizing values generated by the fitted general linear models. Proportional biomass (PB) of species  $j$  at salinity level  $i$  was computed as

$$[2] \quad PB_{ij} = \frac{\text{aboveground biomass of species } j \text{ in mixture}}{\text{aboveground biomass of all three species in mixture}}$$

## Results

Decreases in RTB indicated total biomass losses of 72% for *P. pratensis*, 50% for *H. jubatum*, and 30% for *P. nuttalliana* at the highest salinity level (Fig. 1). Trends in the aboveground to belowground biomass ratio indicated a shift in allocation in *P. pratensis* with increased salinity (Fig. 2). *Hordeum jubatum* showed a less pronounced trend, while *P. nuttalliana* showed little shift in allocation. These results indicate relative salinity tolerance in the order  $P. pratensis < H. jubatum < P. nuttalliana$ .

Sequential (type I) and partial (type III) sums of squares yielded similar results for all three species (Table 1). Residuals for the three models did not deviate significantly from normality ( $P > 0.68$ ) and variances were homogeneous ( $P >$

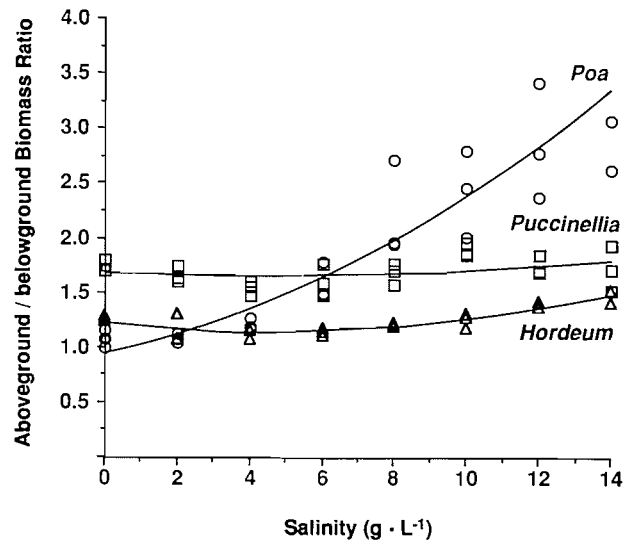


FIG. 2. The effect of salinity on the shoot to root biomass ratio in monocultures of *Poa pratensis*, *Hordeum jubatum*, and *Puccinellia nuttalliana*. Second-order polynomials are fitted to the data.

TABLE 1. General linear model results for the three species.

Species	Treatment	Type I sum of squares		Type III sum of squares	
			$P$		$P$
<i>Poa</i>	C	100.7	<0.001	12.3	<0.001
	S	25.2	<0.001	0.7	0.003
	$S^2$	0.4	0.022	0.4	0.022
	SC	0.8	<0.001	2.8	<0.001
	$S^2C$	4.0	<0.001	4.0	<0.001
<i>Hordeum</i>	C	84.7	<0.001	38.7	<0.001
	S	25.6	<0.001	1.7	<0.001
	$S^2$	0.006	0.766	0.006	0.766
	SC	7.3	<0.001	2.8	<0.001
	$S^2C$	0.9	<0.001	1.0	<0.001
<i>Puccinellia</i>	C	3327.0	<0.001	124.0	<0.001
	S	20.1	<0.001	0.3	0.101
	$S^2$	0.2	0.647	0.02	0.647
	SC	174.6	<0.001	3.13	<0.001
	$S^2C$	3.3	0.079	0.4	0.079

NOTE: Models for each species have 47 df, 42 df for the error term, and one for each of the five model components. C, competition; S, salinity.

0.10). The general linear model provided a very good fit to the data of all three species: *P. pratensis*,  $R^2 = 0.98$ ,  $F = 413.3$ ,  $P < 0.001$ ; *H. jubatum*,  $R^2 = 0.98$ ,  $F = 340.6$ ,  $P < 0.001$ ; *P. nuttalliana*,  $R^2 = 0.99$ ,  $F = 705.1$ ,  $P < 0.001$ . The first-order interaction term ( $SC$ ) was significant for all three species, indicating that the responses of species differed between monoculture and mixture. In addition, the monoculture and mixture curves of *H. jubatum* and *P. pratensis* differed in shape ( $S^2C$  term significant). Plots of aboveground biomass (Fig. 3) reveal that interspecific competition increased the negative response of *P. pratensis* to salinity. *Hordeum jubatum* showed the least reduction in biomass at intermediate salinities, and *P. nuttalliana* responded positively to salinity when grown in mixture. Expressing aboveground biomass in mixture on a proportional basis reveals that *P. pratensis* peaked at the lowest salinity, *H. jubatum* at intermediate levels, and *P. nuttalliana* at the highest salinity (Fig. 4).

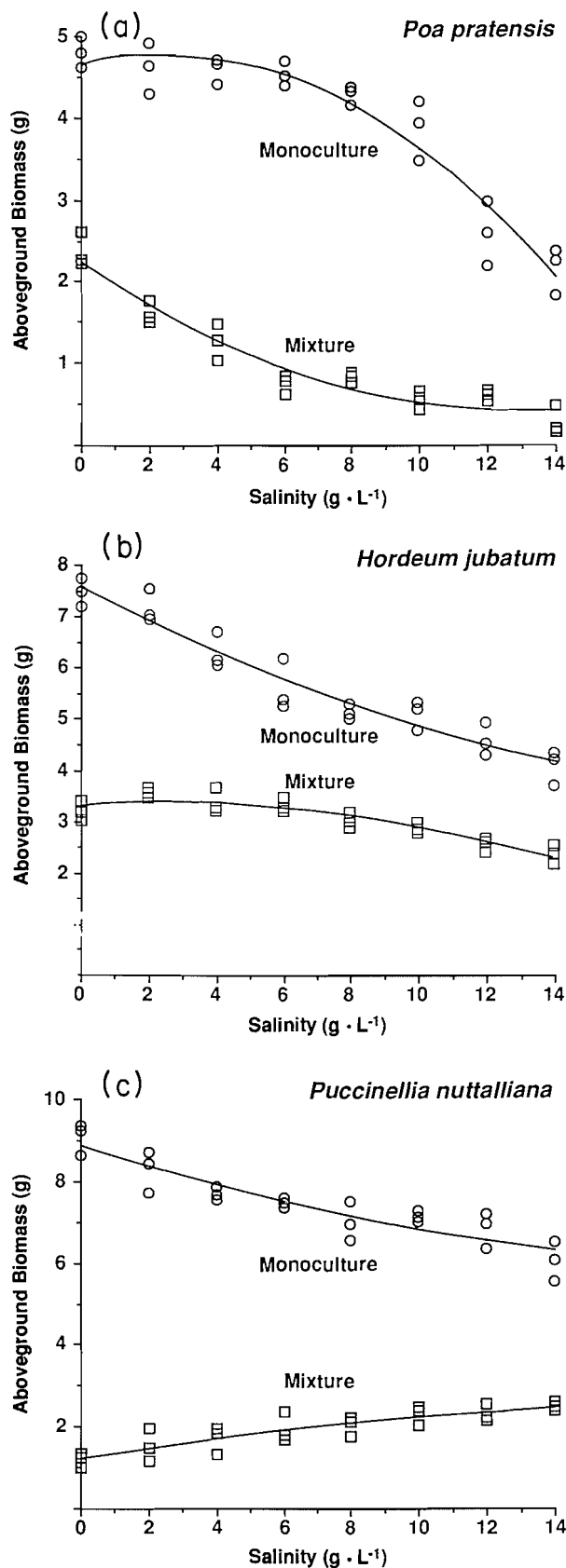


FIG. 3. Response curves (aboveground biomass) for (a) *Poa pratensis*, (b) *Hordeum jubatum*, and (c) *Puccinellia nuttalliana* when grown in monoculture and in mixture. Fitted response curves are second-order polynomials.

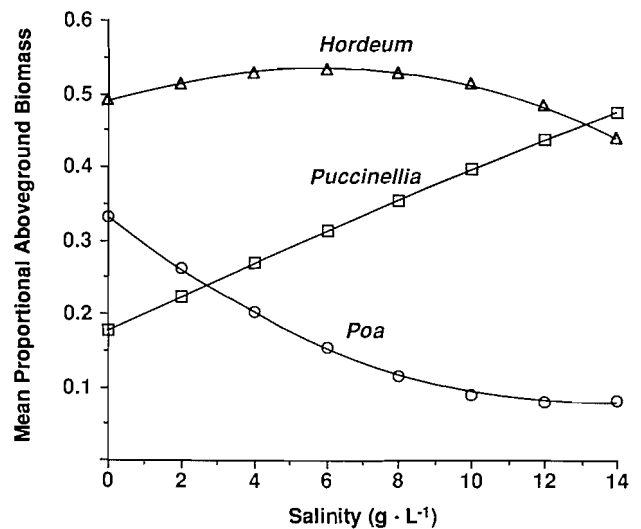


FIG. 4. Mean proportional aboveground biomass (PB) of *Poa pratensis*, *Hordeum jubatum*, and *Puccinellia nuttalliana* when grown in mixture. Values are based on the fitted response curves shown in Fig. 3.

### Discussion

We used an additive experimental design in which each species was grown in monoculture (150 plants/pot) and three-species mixture (150 plants of each species/pot); this allowed us to measure the salinity response of the target species with and without the addition of the other species. For a given target species density, such a design is appropriate for determining the loss in yield of the target species attributable to the presence of other species (Law and Watkinson 1987).

Our results indicate that when grown in monoculture all three grass species performed best at zero salinity. This supports previous results indicating that salt-tolerant grasses are generally facultative rather than "obligate" halophytes (Barbour 1970; Glenn 1987). Each species showed reduced yields with increasing salinity, with the degree of yield reduction indicating relative salinity tolerance in the order *P. pratensis* < *H. jubatum* < *P. nuttalliana*.

Several studies have demonstrated that the aboveground to belowground biomass ratio of salt-tolerant species is less affected by salinity than that of glycophytes (Barbour 1978; Haines and Dunn 1976; Larcher 1980). Why such differential morphological responses to salinity occur is poorly understood, however. The observed changes in aboveground to belowground biomass ratio with increasing salinity (*P. pratensis* > *H. jubatum* > *P. nuttalliana*) support the salinity tolerance ranking based on degree of yield reduction.

Our results also demonstrate that, when grown in mixture, each species has a competitive advantage at different salinity levels: *P. pratensis* at the lowest salinities, *H. jubatum* at intermediate levels, and *P. nuttalliana* at highest salinities. The trade-off between losses attributable to competition and salinity, combined with the differing salt tolerances of species, produced a shift in dominance along the salinity gradient (see Fig. 4) that looked much like that observed in the field (Burchill and Kenkel 1991). The one discrepancy in our experimental results is the relatively consistent performance of *H. jubatum* over all salinities. Seeds of *H. jubatum* are larger than those of the other two species, and observations indicated

that its seedlings had an initial advantage over those of *P. pratensis* and *P. nuttalliana*. This initial advantage appears to have been carried over into the final experimental results. We would predict, however, that growth over several seasons would result in increased dominance of *P. pratensis* at low salinities and of *P. nuttalliana* at high salinities.

We have demonstrated that competition "pushes" salt-tolerant species to the limits of their tolerance range; they are outcompeted in areas where they do best in monoculture. This has been observed in a number of perturbation experiments in saline systems (Silander and Antonovics 1982; Snow and Vince 1984; Ungar et al. 1979; Badger and Ungar 1990). The "sorting out" of species along a salinity gradient, with more tolerant species being competitively displaced to suboptimal regions, can be explained by considering an idealized salinity gradient (Fig. 5a). Species A can grow along the entire gradient, species B at low and intermediate salinities, and species C at low salinities only. If we assume that at low salinities the competitive ability (i.e., the ability to compete for resources with other species) of species C is greater than that of species A and B, then species B can survive in the habitat only if its competitive ability is greater than that of species A at intermediate salinities. The result is that in multispecies mixtures, salt-tolerant species (A and B) show peak performance near their limits of salt tolerance (Fig. 5b). Our experimental results are consistent with this model, implying that competitive ability and salt tolerance are inversely related. Why such a relationship exists remains to be determined, however. One possibility is that in halophytes there is a "physiological trade-off" (Tilman 1988, p. 119) between salt tolerance and competitive ability.

In most studies of salt tolerance, species are grown in monoculture at different salinities. Our results, however, suggest that monoculture experiments cannot successfully predict species performance along a salinity gradient when other species are present. Indeed, we have demonstrated that although all species performed best at the lowest salinity when grown in monoculture (with performance decreasing monotonically with increasing salinity), species responses were significantly different when grown in mixture; the performance of a species along the gradient peaked at the point where the combined effects of interspecific competition and salinity caused the least suppression. This parallels conclusions drawn from dynamic plant community simulation models, which suggest that competitive displacement can lead to the formation of vegetation zones along continuous environmental gradients (Pielou 1974; Czárán 1989; Smith and Huston 1989).

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AUSTIN, M. P., and AUSTIN, B. O. 1980. Behavior of experimental plant communities along a nutrient gradient. *J. Ecol.* **68**: 891–918.

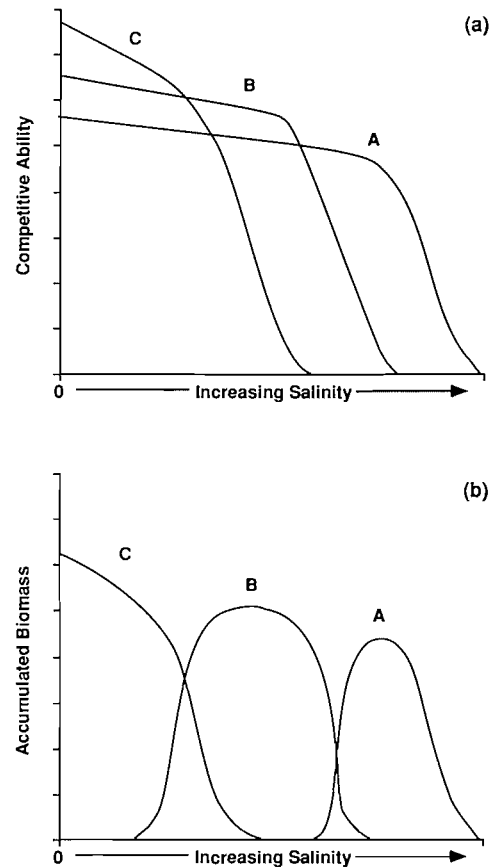


FIG. 5. Hypothetical model of the effect of interspecific competition on the distribution of three grasses along a salinity gradient. (a) Relative competitive ability of three species (A, B, and C) grown in mixture as a function of salinity. (b) The resulting performance (accumulated biomass) of species A, B, and C along the salinity gradient.

- AUSTIN, M. P., GROVES, R. H., FRESCO, L. M. F., and KAYE, P. E. 1985. Relative growth of six thistle species along a nutrient gradient with multispecies competition. *J. Ecol.* **73**: 667–693.
- BADGER, K. S., and UNGAR, I. A. 1990. Seedling competition and the distribution of *Hordeum jubatum* L. along a soil salinity gradient. *Funct. Ecol.* **4**: 639–644.
- BARBOUR, M. G. 1970. Is any angiosperm an obligate halophyte? *Am. Midl. Nat.* **84**: 105–120.
- . 1978. The effect of competition and salinity on the growth of a salt marsh plant species. *Oecologia* (Berlin), **37**: 93–99.
- BEHRINGER, M. 1973. Techniques and materials in biology. McGraw-Hill Book Co., New York, NY. pp. 553–554.
- BERTNESS, M. D., and ELLISON, A. M. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecol. Monogr.* **57**: 129–147.
- BURCHILL, C. A., and KENKEL, N. C. 1991. Vegetation–environment relationships of an inland boreal salt pan. *Can. J. Bot.* **69**: 722–732.
- COOPER, A. 1982. The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytol.* **90**: 263–275.
- CZÁRÁN, T. 1989. Coexistence of competing populations along an environmental gradient: a simulation study. *Coenoses*, **4**: 113–120.
- ELLENBERG, H. 1954. Ueber einige Fortschritte der kausalen Vegetationskunde. *Vegetatio*, **5–6**: 199–211.

- ERNST, W. 1978. Discrepancy between ecological and physiological optima of plant species. A reinterpretation. *Ecol. Plant.* **13**: 175–188.
- FLOWERS, T. J., HAJIBAGHERI, M. A., and CLIPSON, N. J. W. 1986. Halophytes. *Q. Rev. Biol.* **61**: 313–337.
- FREUND, R. J., LITTELL, R. C., and SPECTOR, P. C. 1986. SAS system for linear models. SAS Institute, Cary, NC.
- GLENN, E. P. 1987. Relationship between cation accumulation and water content of salt-tolerant grasses and a sedge. *Plant Cell Environ.* **10**: 205–212.
- HAINES, B. L., and DUNN, E. L. 1976. Growth and resource allocation responses of *Spartina alterniflora* Loisel. to three levels of  $\text{NH}_4\text{-N}$ , Fe and NaCl in solution culture. *Bot. Gaz. (Chicago)*, **137**: 224–230.
- . 1985. Coastal marshes. In *Physiological ecology of North American plant communities*. Edited by B. F. Chabot and H. A. Mooney. Chapman & Hall, New York. pp. 323–347.
- HARPER, J. L. 1982. After description. In *The plant community as a working mechanism*. Edited by E. I. Newman. Blackwell, Oxford. pp. 11–25.
- JOHNSON, W. C., SHARIK, T. L., MAYES, R. A., and SMITH, E. P. 1985. Nature and cause of zonation discreteness around glacial prairie marshes. *Can. J. Bot.* **65**: 1622–1632.
- LARCHER, W. 1980. *Physiological plant ecology*. Springer-Verlag, Berlin.
- LAW, R., and WATKINSON, A. R. 1987. Response–surface analysis of two-species competition: an experiment on *Phleum arenarium* and *Vulpia fasciculata*. *J. Ecol.* **75**: 871–886.
- MACKE, A. J., and UNGAR, I. A. 1971. The effects of salinity on germination and early growth of *Puccinellia nuttalliana*. *Can. J. Bot.* **49**: 515–520.
- MEAD, R. 1988. *The design of experiments. Statistical principles for practical applications*. Cambridge University Press, Cambridge.
- MUELLER-DOMBOIS, D., and SIMS, H. P. 1966. Response of three grasses to two soils and a water table depth gradient. *Ecology*, **47**: 644–648.
- NETER, J., and WASSERMAN, W. 1974. *Applied linear statistical models*. R. D. Irwin, Homewood, IL.
- PICKETT, S. T. A., and BAZZAZ, F. A. 1978. Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology*, **59**: 1248–1255.
- PIELOU, E. C. 1974. Competition on an environmental gradient. In *Mathematical problems in biology*. Edited by P. van den Driessche. Lecture notes in biomathematics. Vol. 2. Springer-Verlag, Berlin. pp. 184–204.
- POTVIN, C., LECHOWICZ, M. J., BELL, G., and SCHOEN, D. 1990. Spatial, temporal and species-specific patterns of heterogeneity in growth chamber experiments. *Can. J. Bot.* **68**: 499–504.
- SAS INSTITUTE INC. 1985. *SAS user's guide: statistics, version 5*. SAS Institute Inc., Cary, NC.
- SILANDER, J. A., and ANTONOVICS, J. 1982. Analysis of interspecific interactions in a coastal plant community — a perturbation approach. *Nature (London)*, **298**: 557–560.
- SMITH, T., and HUSTON, M. 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, **83**: 49–69.
- SNEDECOR, G. W., and COCHRAN, W. G. 1967. *Statistical methods*. 6th ed. Iowa State University Press, Ames, IA.
- SNOW, A. A., and VINCE, S. W. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *J. Ecol.* **72**: 669–684.
- TILMAN, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, NJ.
- UNGAR, I. A. 1974a. Inland halophytes of the United States. In *Ecology of halophytes*. Edited by R. J. Reinhold and W. H. Queen. Academic Press, New York, NY. pp. 235–306.
- . 1974b. The effect of salinity and temperature on seed germination and growth of *Hordeum jubatum*. *Can. J. Bot.* **52**: 1357–1362.
- . 1987. Population ecology of halophyte seeds. *Bot. Rev.* **53**: 301–334.
- UNGAR, I. A., BENNER, D. K., and MCGRAW, D. C. 1979. The distribution and growth of *Salicornia europaea* on an inland salt pan. *Ecology*, **60**: 329–336.