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SPECIES COMPETITIVE ABILITY AND POSITION ALONG A NATURAL STRESS/DISTURBANCE GRADIENT¹

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Abstract. We tested the prediction that plant species that grow in undisturbed, nutrient-rich habitats tend to have higher competitive abilities than those found in disturbed or nutrient-poor habitats. The distributions of seven species (*Eriocaulon septangulare*, *Rhynchospora fusca*, *Hypericum ellipticum*, *Juncus pelocarpus*, *Lysimachia terrestris*, *Dulichium arundinaceum*, and *Drosera intermedia*) were measured along a gradient of exposure to wave action on the shore of Axe Lake, Ontario. The exposure gradient incorporates disturbance, through the removal of plant biomass, and stress, through the creation of a gradient in sediment organic content, nutrient concentrations, and fine particle sizes. Species distributions on the exposure gradient were quantified by determining the mean sediment organic content of the quadrats containing each species. Competitive abilities were measured as relative increase in dry mass per plant, in a field experiment in which species were grown together in all pairwise combinations ($N = 10$ replicates). Species had significantly heterogeneous competitive abilities ($P < .01$). Species found on exposed, nutrient-poor shores (e.g., *E. septangulare*) had low competitive abilities, while those growing on sheltered, nutrient-rich shores (e.g., *D. arundinaceum*) had high competitive abilities. Competitive ability was significantly correlated with mean position on the exposure gradient.

Key words: Axe Lake, Ontario; competitive ability and distribution; exposure to waves; marshes; shoreline plants; stress and disturbance gradient; wetlands; zonation.

INTRODUCTION

Grime (1973, 1977) predicted that species found in undisturbed, nutrient-rich habitats should have high competitive abilities relative to species found in more disturbed or stressful habitats. Models of species diversity proposed by Connell (1978) and Huston (1979) also imply that species occurring in infrequently disturbed habitats should have high competitive abilities. While the role of interspecific competition in determining species distributions along environmental gradients has received experimental attention (e.g., Sharitz and McCormick 1973, Mueller-Dombois and Ellenberg 1974:354, Pickett and Bazzaz 1978, Austin and Austin 1980, Grace and Wetzel 1981, Austin 1982, Parrish and Bazzaz 1982, Silander and Antonovics 1982, del Moral 1983, Snow and Vince 1984, Austin et al. 1985, Goldberg 1985), no test of this proposed relationship between species competitive abilities and distributions has been performed for a multispecies community. We examined the prediction that species' distributions along an environmental gradient are related to their competitive abilities. We first described the field distributions of seven plant species along a natural environmental gradient that incorporates both stress and disturbance (*sensu* Grime 1979). We then measured the competitive abilities of the same species in a nutrient-rich, undisturbed habitat using a diallel experiment (Harper 1977:267). Lastly, we tested for a correlation between competitive ability and mean position on the environmental gradient.

METHODS

The environmental gradient

The environmental gradient chosen for study was the gradient of exposure to wave action that runs parallel to the waterline of small lakes. Horizontal variation in the abundance of plant species along the exposure gradient has been described by Pearsall (1920), Thunmark (1931), Keddy (1983), and Wilson and Keddy (1985). Exposure is a complex gradient that has both stress and disturbance components. Disturbance is produced by the direct effect of wave action removing biomass more rapidly from exposed shores than from sheltered shores. Exposed shores are also stressful because relatively high levels of wave action there produce sediments with low organic matter content, low nutrient concentrations, and coarse particle sizes (Keddy 1985). The exposure gradient is characterized at one end by wave-washed, sparsely vegetated, nutrient-poor beaches and at the other by sheltered, densely vegetated, nutrient-rich bays. In this study, position on the exposure gradient was quantified by measuring sediment organic matter content (Wilson and Keddy 1985); sediment organic matter content, nutrient concentration, and fine particle sizes are all significantly negatively correlated with exposure (Keddy 1985). The exposure gradient and associated plant communities at Axe Lake have been described by Keddy (1981, 1983).

Field distributions

The distributions of seven vascular plant species, *Eriocaulon septangulare*, *Rhynchospora fusca*, *Hypericum ellipticum*, *Juncus pelocarpus*, *Lysimachia terrestris*, *Dulichium arundinaceum*, and *Drosera intermedia* (nomenclature follows Gleason and Cronquist 1963) were measured along the exposure gradient on

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the shoreline of Axe Lake, Ontario. Species distributions along the exposure gradient were described by breaking down the range of sediment organic matter content into seven classes (class 1: 0.0–0.9%, class 2: 1.0–1.9%, class 3: 2.0–3.9%, class 4: 4.0–7.9%, class 5: 8.0–15.9%, class 6: 16.0–31.9%, class 7: >32.0%) and calculating the relative frequency of occurrence of the seven study species in each class. Quadrats (0.5×0.5 m, $N = 243$) were placed at 10-m intervals along the waterline of Axe Lake during 17–21 August 1984 and the presence of all species in each quadrat was recorded. Organic matter content of a sediment sample from the center of each quadrat was determined and the sample categorized by the classes described above. Sediment samples (3.5 cm diameter, 5 cm deep) were frozen at -10°C within 1 wk of collection and analyzed for organic content 1 mo later (Dean 1974). Organic content is expressed as a percentage of sample dry mass. The mean position of each species on the exposure gradient was determined by calculating the mean sediment organic content value for the set of quadrats containing each species.

Competitive abilities

Competitive abilities were measured in a diallel experiment (Harper 1977) on the shore of Axe Lake. Polypropylene beakers (400 mL, diameter = 8.5 cm) were filled with a bottom layer of 200 mL of sand and a top layer of 200 mL of organic shoreline sediment obtained from a sheltered shore of Axe Lake. This potting medium simulated the natural stratification of sediments on sheltered shores. Plants were collected on 18–20 May 1984. Ramets of each species of approximately equal size were selected and a subset of 10 was randomly chosen for initial dry mass determination. On 21–22 May, ramets were randomly assigned to beakers to produce 10 replicates each of all possible pairwise combinations with two ramets per beaker. Beakers were placed on flats on the shore just above the waterline in a sheltered bay, and watered daily with lake water. A cylinder of fiberglass window screen 15 cm high was installed in each beaker on 28 June to ensure that ramets interacted only with the neighbor in its own beaker and did not influence the growth of plants in other beakers. The experiment was harvested during 1–4 September 1984. Plants were dried to constant mass, and the total biomass of each species in each beaker was measured.

Competition experiment results may be given as relative yield per plant (Harper 1977:260, Fowler 1982) in order to compare the yields of species of different sizes. Because we used vegetatively reproducing ramets, however, the relative increase of dry mass per plant (RIP) was of greater interest than relative yield. Relative increase per plant was calculated as

$$\text{RIP}_{ij} = (\text{HDM}_{ij} - \text{SDM}_i)/(\text{HDM}_{ii} - \text{SDM}_i),$$

where RIP_{ij} is the relative increase per plant of species

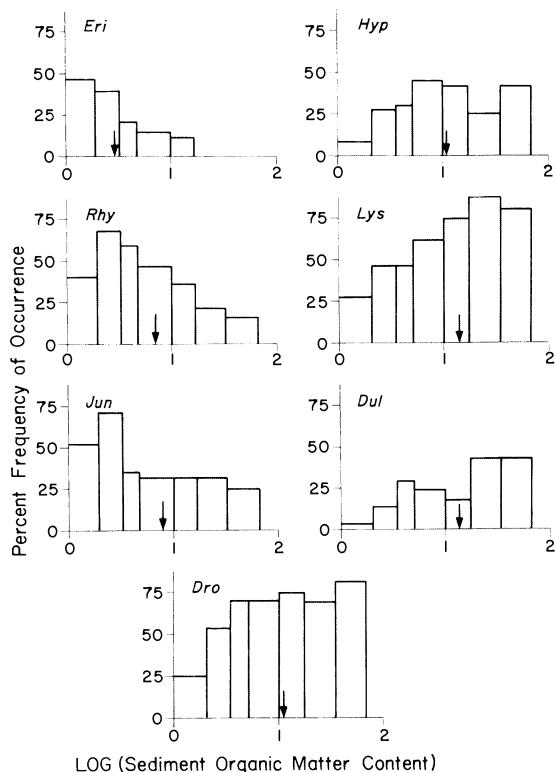


FIG. 1. The distributions of seven plant species along the exposure gradient at Axe Lake, Ontario. Exposure is measured as percent organic matter of the sediment (Wilson and Keddy 1985). The mean sediment organic content associated with each species is indicated by an arrow. Species' names are abbreviated as follows: Eri: *Eriocaulon septangulare*, Rhy: *Rhynchospora fusca*, Jun: *Juncus pelocarpus*, Hyp: *Hypericum ellipticum*, Dro: *Drosera intermedia*, Lys: *Lysimachia terrestris*, Dul: *Dulichium arundinaceum*.

i when grown with species j , HDM_{ij} is the harvested dry mass of one ramet of species i when grown with one ramet of species j , SDM_i is the mean starting dry mass of one ramet of species i , and HDM_{ii} is the mean harvested dry mass of one ramet of species i when grown with a conspecific neighbor. Thus the RIP of a ramet grown with another of the same species is 1. A ramet may have $\text{RIP} < 1$ or > 1 when grown with a ramet of another species. An RIP value < 1 suggests that a species accumulates less biomass in the presence of an interspecific neighbor than with a conspecific neighbor. An RIP value > 1 suggests that the species accumulates more biomass when grown with an interspecific neighbor than with a conspecific neighbor.

Diallel experiments provide two measures of competitive ability. The first is the mean RIP of each species when grown with all species of neighbors. This mean RIP may be termed the target score because it is a measure of the mean effect of all species of neighbors on the species acting as a target. A species has a high target score if, on average, it grows better with all other species than with itself. A species has a low target score

TABLE 1. Relative increase in dry mass per plant (RIP) of seven species* grown in all pairwise combinations from late May to early September.

Target species	Neighbor species							Target scores†
	Dul	Jun	Lys	Hyp	Rhy	Dro	Eri	
Dul	1.00	1.33	1.18	1.17	1.25	1.18	1.34	1.20 ^{ab}
Jun	0.63	1.00	1.34	1.46	1.46	1.52	1.49	1.28 ^a
Lys	0.88	0.87	1.00	1.63	1.63	1.78	1.57	1.31 ^a
Hyp	1.09	0.99	0.91	1.00	1.22	1.29	1.23	1.11 ^{abc}
Rhy	1.05	0.73	0.93	0.91	1.00	1.21	1.36	1.03 ^{bc}
Dro	0.98	0.91	0.93	1.02	1.02	1.00	1.11	0.98 ^{bc}
Eri	0.65	0.71	0.88	0.89	0.87	1.48	1.00	0.93 ^c
Neighbor scores†	0.89 ^a	0.93 ^{ab}	1.03 ^{abc}	1.15 ^{bcd}	1.21 ^{cd}	1.35 ^d	1.30 ^d	

* Species names abbreviated as in Fig. 1.

† Target score is the mean RIP of each species when grown with all six species of neighbors. Neighbor score is the mean RIP of all target species with which a particular neighbor species was grown. Target and neighbor scores not significantly different from one another (Tukey's Studentized range test, $P < .05$) are denoted by common superscripts.

if, on average, the species grows less well with all other species than with itself. The species can be ranked in order of competitive ability using target scores such that strong interspecific competitors have high target scores and subordinate competitors have lower scores.

The second measure of competitive ability produced by this analysis is the mean RIP associated with each species acting as a neighbor on all target species. The mean RIP of all target species with which a particular neighbor species was grown is called the neighbor score for that neighbor species. A species has a high neighbor score if, on average, other species tend to grow better with that interspecific neighbor than with themselves. A species has a low neighbor score if other species tend to grow less well with the interspecific neighbor than with themselves. Thus, species can be ranked in order of their competitive abilities using their neighbor scores such that strong competitors have low neighbor scores (because they suppress target species) and subordinate competitors have higher neighbor scores (because they release target species). Target and neighbor scores may be negatively correlated (Jacquard 1968).

A two-factor analysis of variance was used to test for significant target and neighbor effects. No transformation was found to produce homoscedasticity of variances. The results of the analysis should therefore be interpreted with caution, although Ito (1980) states that ANOVA is extremely robust under heteroscedastic conditions when sample sizes are large and equal, and dimensionality is low. Tukey's Studentized range test was used to identify groups of species not significantly different in competitive ability.

Competitive abilities and field distributions

Correlations were calculated between mean position on the exposure gradient and both measures of competitive ability (target and neighbor scores) using one-tailed Pearson's r . To test the significance of the correlation between mean position and overall competitive ability, the probabilities associated with the

correlations between position and both target and neighbor scores were combined (Sokal and Rohlf 1969). Correlations were then calculated for the complete set of seven species and for the set with the one insectivorous species, *Drosera intermedia*, excluded.

RESULTS

Field distributions

Eriocaulon septangulare occurred most frequently on exposed shores with low organic content while *Lyssimachia terrestris* and *Dulichium arundinaceum* were most common on sheltered shores with high organic content (Fig. 1). Others, such as *Rhynchospora fusca* and *Juncus pelocarpus*, had intermediate distributions.

Competitive abilities

Table 1 shows the RIP of each species grown in all possible pairwise combinations. ANOVA (Table 2) showed significant effects ($P < .01$) for both target scores (rows in Table 1) and neighbor scores (columns). Groups of species not significantly different in competitive ability are given in Table 1.

Competitive abilities and field distributions

A significant correlation was found between competitive ability and mean position on the exposure gradient for the set of species excluding the insectivorous *Drosera intermedia* (correlation between competitive ability measured as target scores and position: $r = 0.77$, $P = .035$; correlation between competitive ability measured as neighbor scores and position: $r = -0.68$, $P = .068$; combined probability: $\chi^2 = 12.07$, $.01 < P < .025$) (Fig. 2). A weaker relationship was found when *D. intermedia* was included in the analysis (target scores: $r = 0.61$, $P = .071$; neighbor scores: $r = -0.36$, $P = .211$).

DISCUSSION

The diallel experiment demonstrates that the study species have significantly heterogeneous competitive

TABLE 2. Two-factor analysis of variance of diallel plant competition experiment. Target and neighbor scores are given in Table 1.

Source	df	ss	MS	F	P
Target scores	6	9.37	1.56	7.79	.01
Neighbor scores	6	13.37	2.23	11.11	.01
Error	461	92.47	0.20		
Total	473	115.22			

abilities. There are many factors, however, that may influence species ranking within a competitive hierarchy produced by an experiment. Probably the most important of these is the environment in which the experiment is conducted (Harper 1977). Fowler (1982) found that the dominance hierarchy described by diallel experiments varied with water availability and time of year. Moore and Williams (1983) showed that the competitive hierarchy within a group of weedy species varied with soil nutrients. We used an experimental environment representing sheltered bays: that portion of the exposure gradient where plants accumulate biomass most rapidly (Wilson and Keddy 1985) and disturbance is minimal (Keddy 1985). Community standing crop and diffuse competition are also highest in this habitat (Wilson and Keddy 1986) and competitive ability is presumably most important for success in this type of environment. Our results do not exclude the possibility that competitive dominance varies with position on the exposure gradient (Tilman 1985).

Competitive hierarchies may also vary seasonally: our experiment was performed during the only time of the year the plants are capable of growth, since the shoreline is covered by deep water, ice, and snow from October to May. Further, this experiment considered only pairwise species interactions and may not provide information about the species' relative aggressiveness in multispecies mixtures. Lastly, Inouye and Schaffer (1981) note that the outcome of any replacement series experiment (many of which comprise a diallel experiment) may vary with total density. Aarssen (1985) has also warned against comparing the suppression of two species when the carrying capacities for the species in the experiment are unknown. The competitive hierarchy described by this experiment is likely unique to the particular starting density used. In summary, while diallel experiments have clearly recognized limitations, they do allow among-species comparisons of competitive ability while controlling for density, abiotic factors, and neighbors (McGilchrist 1965, Norrington-Davies 1967, Harper 1977, Fowler 1982).

The use of mean RIP values (target and neighbor scores) as a measure of competitive ability should be interpreted with caution, because RIP may be >1 for two distinct reasons. RIP > 1 may indicate (1) that one species has outcompeted the other; or (2) that the species of interest exploits a different array of resources than its interspecific neighbor. In the second case, RIP

is attributable to niche differentiation (L. W. Aarssen, personal communication). In contrast, RIP values <1 (suppression) can only be attributed to interspecific competition. An alternative analysis of competitive ability that avoids confusion between competitive ability and niche differentiation is to consider only RIP values that are attributable to competitive suppression, i.e., cases where RIP < 1 . Therefore, we have also estimated the competitive ability of each species as the number of neighboring species that suppressed its growth. Species were ranked from strong competitors, which were rarely suppressed, to weak competitors, which were frequently suppressed. The number of suppressions for each species was subtracted from the total number of species in the experiment, so that species with high competitive abilities received high scores and those with low abilities received low scores. The correlation between this measure of competitive ability

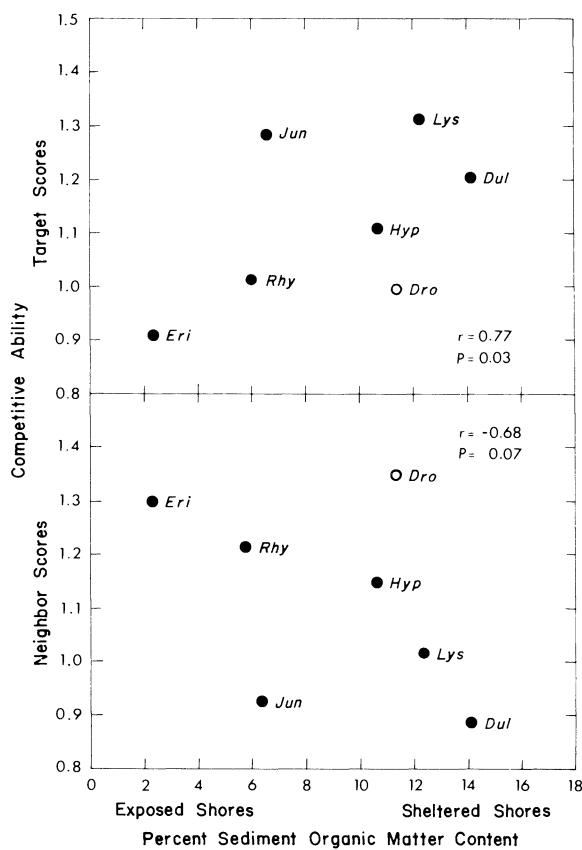


FIG. 2. The relationship between the competitive abilities of seven plant species and their mean positions on the exposure gradient. Competitive abilities were measured as target scores (the mean relative increase in dry mass of a species grown in the presence of all six species of neighbors) and as neighbor scores (the mean relative increase in dry mass of all six species in the presence of a particular target species). Correlation values are given for the set of species excluding the insectivorous *Drosera intermedia*. Species names are abbreviated as in Fig. 1.

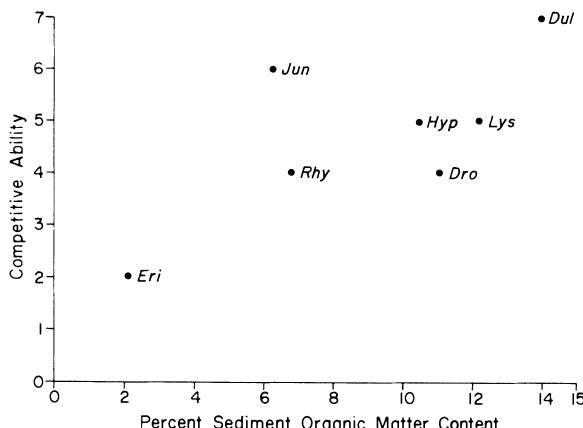


FIG. 3. The relationship between the competitive abilities of seven plant species and their mean positions on the exposure gradient, where the competitive ability of each species is calculated as the number of neighbor species by which it is suppressed (see Discussion). Relative competitive ability is correlated with position on the exposure gradient ($r = 0.71$, $P < .05$). Species names are abbreviated as in Fig. 1.

and mean position on the exposure gradient was then tested using one-tailed Pearson's r . Fig. 3 shows that competitive ability was significantly correlated with position on the exposure gradient ($r = 0.71$, $P < .05$). These results agree with those given in Fig. 2.

Fig. 2 shows that species with high competitive abilities occupy sheltered, nutrient-rich shores while species with low competitive ability are characteristic of disturbed, sandy habitats. This relationship is significant, however, only when the insectivorous *Drosera intermedia* is excluded from consideration; *Drosera* has low competitive ability but is found on relatively undisturbed, organic shorelines. Wilson (1985) has shown experimentally that insectivory allows *Drosera* to avoid competitive suppression by exploiting a nutrient source unavailable to other species. Evidence that the growth of *Drosera* is unaffected by other species is given in Table 1 by the target scores for *Drosera*. RIP is ≈ 1 for this species acting as a target, indicating that *Drosera* grows as well with any other species as it does with itself. The ability of *Drosera* to use insects as a nutrient source may allow this small rosette species (1–8 cm high, Gleason and Cronquist 1963) to grow in undisturbed, densely vegetated habitats, accounting for its position in Fig. 2. In contrast, the study species most morphologically similar to *Drosera*, *Eriocaulon septangulare*, is restricted to disturbed habitats with low standing crop (Fig. 2).

Considerable variability remains in the relationship shown in Fig. 2 even when *D. intermedia* is excluded. This variability is partly due to problems inherent in the measurement of competitive ability discussed above. There may also exist variability in the relative positions of the species along the exposure gradient produced by the use of presence-absence data to mea-

sure distributions: examination of the distribution of biomass of each species along the exposure gradient might produce different results. Lastly, a perfect relationship should perhaps not be expected, since relative competitive abilities are almost certainly not the only determinant of species distributions along an environmental gradient. The relative importance of dominance hierarchies in determining species distributions along gradients remains to be explored.

Previous experimental work has described the role of competition in producing zonation patterns (e.g., Connell 1961, Austin and Austin 1980, Lubchenco 1980, Grace and Wetzel 1981), but the relationship between position in a competitive hierarchy and distribution along a natural gradient for multiple-species sets has not been examined. Studies that have considered this relationship have estimated competitive ability using species characters likely to be related to competitive success. Grime and Hunt (1975) examined the relationship between maximum potential growth rates and field distributions within a local flora. As they noted, however, high growth rates are found in both competitive and ruderal species. Boorman (1982) also suggested that a relationship might exist between growth rates and the distributions of sand dune plants. Menges and Waller (1983) used published maximum heights to relate competitive ability to occurrence in productive, undisturbed habitats within a floodplain. Experimentally measured competitive abilities allow a direct test of the predicted relationship between competitive ability and distribution.

Yodzis (1978) has discussed the effects of disturbance on community structure. He notes that the shape of diversity-disturbance relationships would depend on the competitive relationships of the species removed by disturbance. In particular, if disturbance removed competitive dominants, then intermediate levels of disturbance could lead to increased species diversity (see Grime 1979, Huston 1979). Alternatively, if disturbance removed competitive subordinates, then diversity should simply decrease with increasing disturbance. Our data (Fig. 2) suggest that disturbance eliminates competitive dominants, thereby allowing competitive subordinates to occupy more disturbed or stressed sites. The diversity-disturbance relationship in shoreline plant communities is also consistent with this postulated mechanism. Species richness reaches a maximum at intermediate levels of disturbance in Axe Lake (Keddy 1983). A similar, but weaker, intermediate disturbance relationship has also been documented on a second lakeshore exposure gradient (Keddy 1984). There may be a basic morphological explanation for disturbance selectively removing competitive dominants. The very attributes that contribute to competitive dominance (such as tall, leafy shoots; Grime 1979) may make them susceptible to wave damage. Conversely, the morphologies most resistant to wave damage (small rosettes) may be weak competi-

tors, since they are unable to shade taller species. This could be the mechanism producing the situation postulated by Yodzis (1978), where competitive dominants are selectively reduced by disturbance.

In conclusion, our results suggest that the competitive abilities of plant species may vary predictably, so that superior competitors are frequently found in habitats where stress and disturbance (*sensu* Grime 1979) are minimal and diffuse competition is intense (Wilson and Keddy 1986). Because stress and disturbance vary along other environmental gradients (e.g., altitude on mountains, height in the rocky intertidal zone, depth in the abyssal seas), competitive hierarchies may be correlated with zonation patterns in other multispecies communities.

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