*Ecology*, 76(1), 1995, pp. 280–291

# COMPETITIVE PERFORMANCE AND SPECIES DISTRIBUTION IN SHORELINE PLANT COMMUNITIES: A COMPARATIVE APPROACH[1]

Connie L. Gaudet and Paul A. Keddy[2]
*Department of Biology, University of Ottawa, P.O. Box 450 Station A,*
*Ottawa, Ontario, Canada K1N 6N5*

*Abstract.* Using a comparative approach, we tested the prediction that relative competitive performance of plant species is correlated with distribution along natural gradients of fertility and standing crop. The mean position of 40 species of herbaceous plants along standing crop, phosphorus, nitrate, magnesium, potassium, pH, and percent organic content gradients was calculated based on data from 217 quadrats from lake and river shorelines in Nova Scotia, Quebec, and Ontario. Competitive performance was measured in an outdoor experiment in which species were grown together with a common phytometer, *Lythrum salicaria* ($n = 5$ replicates per species). The relative ability of each species to suppress the growth of the phytometer was used as a measure of relative competitive performance. This measure of competitive performance was significantly correlated with the mean position of species on the standing crop ($r = 0.081$; $P < 0.0001$), percent organic content ($r = 0.71$; $P < 0.0001$); phosphorus ($r = 0.70$; $P < 0.0001$), nitrate ($r = 0.67$; $P < 0.0001$), magnesium ($r = 0.66$; $P < 0.0001$), and potassium gradients ($r = 0.61$; $P < 0.0001$). When monocotyledons and dicotyledons were considered separately, the relationship between distribution along the macronutrient gradients and competitive performance was much stronger for monocotyledons. It is suggested that this may reflect a differential influence of disturbance on distribution.

*Key words: competition; competitive ability; resource gradients; shoreline plant communities; standing crop gradient.*

## INTRODUCTION

The assumption that competitive ability varies along natural environmental gradients of fertility and standing crop is implicit in many general models of plant community structure (Ellenberg and Mueller-Dombois 1974, Grime 1977, 1979, Tilman 1982, 1985, 1988, Austin 1986, Ellenberg 1988, Southwood 1988, Keddy 1990*a*, *b*, Keddy and MacLellan 1991) such that the interaction between competitive ability, resource availability, and disturbance determines vegetation composition (Austin 1986, Campbell and Grime 1992, Turkington et al. 1993). Despite its central importance to plant community theory, the basic relationship between competitive ability and distribution along natural environmental gradients has rarely been tested empirically at a scale that enables generalization beyond the particular study conditions or species.

It is becoming increasingly apparent that properties or processes emergent at one level or scale of interaction may not be predictable from lower scales of interaction (e.g., O'Neill et al. 1986, Allen 1987, Moore and Keddy 1989, Reader et al. 1994). Field experiments may be conducted at many different scales, and at many different locations along an environmental gradient, yielding what often appear to be contradictory results in the development of general competition theory (e.g., Wilson and Shay 1990, Wilson and Tilman 1991, Campbell and Grime 1992, Goldberg and Barton 1992, Turkington et al. 1993). The current study therefore emphasizes a test of the generality of the relationship between competitive ability and distribution at a broad community scale, across a large number of species and sites, and a broad range of resource availability. To enable a test of this relationship at such a broad scale, we explore the use of a relatively novel screening or comparative approach (Grime 1977) for evaluating relative competitive performance for a large number of species (Gaudet and Keddy 1988). Specifically, we tested the hypothesis that species distributions along natural environmental gradients of fertility and standing crop are related to their relative competitive performance. We provide a simple, direct test of the importance of this predicted relationship as the basis for further development of predictive (sensu Peters 1982) theory about community pattern and process.

Shoreline plant communities are highly suited as a test of this relationship. Species composition has been shown to vary along natural environmental gradients of stress and disturbance related to wave exposure in shoreline communities (Keddy 1983, 1984). Grace and Wetzel (1981) and Snow and Vince (1984) present evidence that competition produces zonation patterns in marshes, and Wilson and Keddy (1986*a*) have shown

---

[1] Manuscript received 28 September 1993; revised 4 May 1994; accepted 5 May 1994.

[2] Send reprint requests to this author.

that, for specific sites, competition intensity increases along a gradient of soil organic content and that the mean position of species along this gradient is related to relative competitive performance (Wilson and Keddy 1986*b*). This last experiment had only seven species and a single environmental measure (percent soil organic content). Whereas mineral nutrient levels can be directly considered as environmental gradients of resource availability, standing crop and percent organic content are emergent community properties (Austin and Smith 1989). Standing crop is a complex response variable that integrates abiotic factors such as resource availability, exposure, and disturbance, and biotic interactions (Grime 1979, Wilson and Keddy 1986*b*), and this measure is emerging as a key state variable in predictive community ecology along which important community properties such as competition intensity and species richness vary (e.g., Grime 1979, Wilson and Keddy 1986*b*). It is, however, difficult to interpret the underlying contribution of environmental resource gradients in studies using only standing crop as a predictor variable, or to compare across studies using different measures of productivity or fertility. Here, we provide a direct test of the relationship between competitive performance and field distribution not only along the standing crop and percent soil organic content gradient, but along environmental resource gradients of fertility (soil phosphorus, magnesium, potassium, nitrate), and pH.

The usual approach to measuring competitive performance is to assess the performance (relative yield) of species in all possible pair-wise combinations (e.g., Harper 1977, de Wit 1960). This approach is logistically demanding and limits the number of species that can be tested. To increase the number of species that could be examined, we used a "phytometer" or indicator (Clements 1933) approach based on a modified additive design (Harper 1977) in which the relative competitive performance of a species is evaluated by measuring the relative performance to suppress the growth of a common indicator or background species (phytometer). Although relatively novel in plant community ecology, a bioassay or indicator approach is a useful approach for examining a large number of species with diverse morphologies (e.g., Grime and Hunt 1975, Reader and Southwood 1981, McCanny et al. 1990). The advantage of the phytometer approach is that it provides directly, values of competitive performance on an arbitrary scale for a large number of species. Though this method has received little experimental attention in studies of plant competition (except see Welbank 1963, Mitchley and Grubb 1986), it is highly suited to the current research with emphasis on a comparative screening of a large number of species.

## METHODS

### *Study locations*

To maximize generality, sampling areas were selected from a broad geographic region, including both lake and river shorelines and inland marsh. Sites encompassed a broad range in standing crop and species composition representative of emergent shoreline plant communities in northeast North America. One group of wetlands occurred in the Tusket River Valley in Yarmouth County, Nova Scotia. Wilsons Lake and Ellenwood Lake (43°55′ N, 65°53′ W) in the Tusket River system have sandy, gravel and boulder shorelines characterized by exceptional species richness and the presence of many rare and endangered species (Wisheu 1987, Wisheu and Keddy 1989). A second wetland represented the Georgian Bay area of Ontario. Axe Lake (45°23′ N, 79°30′ W), a remnant of the shoreline of glacial Lake Algonquin, is a small, sandy lake that supports a rich Atlantic coastal plain flora (Keddy 1981, 1983). The third group of wetlands were located in the Ottawa River watershed; a general description of these wetland types can be found in Day et al. (1988), Shipley (1987), Shipley et al. (1991), and Moore (1990). The Westmeath study location (45°47′ N, 76°50′ W) is a riverine shoreline located on the Ottawa River 22 km southwest of the city of Pembroke. At this location, two open beach sites with low standing crop as well as three moderate to high standing crop sites in a sheltered bay were surveyed. A very high standing crop *Typha* marsh located 15 km south of Westmeath was also surveyed. The Luskville study location (45°31′ N, 76°6′ W) is also a riverine shoreline located 5 km west of Luskville, Quebec on the Ottawa River. The survey included two low standing crop shoreline sites, moderate and high standing crop sheltered marshes and a very high standing crop *Typha* marsh (see Moore 1990). Several smaller sites were also sampled along the Ottawa River. Breckenridge and Lucerne Boulevard are moderate standing crop sites on the Ottawa River ≈5 km and 30 km east of the Luskville site, respectively. The Ottawa Beach site is also located on the Ottawa River, ≈1 km west of Ottawa, Ontario. Stony Swamp is a large wetland complex comprised of several beaver ponds and is located ≈10 km inland from the Ottawa Beach site in Nepean, Ontario.

Collectively, these sites encompassed a broad range in plant life form. Plant life history types included evergreen rosette species (e.g., *Lobelia dortmanna, Eriocaulon septangulare*), insectivorous species (e.g., *Drosera intermedia),* reeds (e.g., *Scirpus validus, Eleocharis palustris*), annuals (e.g., *Bidens cernua*), facultative annuals (e.g., *Lythrum salicaria*) and large clonal perennials (e.g., *Typha latifolia, Phalaris arundinacea*). In general, low standing crop sites such as Axe and Wilsons Lake are characterized by species of varying life form (e.g., annuals, evergreen, and slow-growing perennials) while high standing crop areas are dominated by fast-growing perennials capable of clonal spread.

### *Field survey*

The study locations were surveyed as follows: Westmeath (25–26 August 1987); Luskville (18–19 August

TABLE 1. Correlation ($r_s$) between all measured environmental variables from all study sites ($n = 217$ quadrats). SC = aboveground standing crop; % org = soil percent organic content; P = soil phosphorus content; K = soil potassium

| | % org | | P | | N | |
|---|---|---|---|---|---|---|
| | $r$ | $P$ | $r$ | $P$ | $r$ | $P$ |
| SC (g/0.25 m$^2$) | 0.77 | $P < 0.00001$ | 0.76 | $P < 0.00001$ | 0.66 | $P < 0.00001$ |
| % org | | | 0.77 | $P < 0.00001$ | 0.57 | $P < 0.00001$ |
| P (mg/kg) | | | | | 0.72 | $P < 0.00001$ |
| N (mg/kg) | | | | | | |
| K (mg/kg) | | | | | | |
| Mg (mg/kg) | | | | | | |

1987); Wilsons Lake and Ellenwood Lake (7–8 October 1988); all other sites between 26 August and 6 September 1988). At each site or standing crop increment, 5–15 quadrats (0.5 × 0.5 m) were placed using a restricted randomization procedure over an area of ≈100 m$^2$. Areas that were obviously disturbed or transition zones between wetland and upland areas were not sampled. After the quadrat was placed on the ground, each quadrat was subdivided into nine equivalent sections using thin metal rods. The frequency of each species within the quadrat was then measured as the number of subsections (0–9) in which it occurred. This frequency method was selected to maximize the efficiency of sampling effort while at the same time enabling an evaluation of the relative abundance of species along the environmental gradient (Goldsmith and Harrison 1976). For a study of this scale, this approach was considered a reasonable compromise between sampling methods such as point cover and biomass determination, which provide detailed information on distribution but are labour intensive, and simple presence/absence approaches. After the species occurrence and frequency was recorded for each quadrat, the vegetation within the quadrat was clipped at ground level, dried to constant biomass at 60°C, and weighed to determine standing crop. All voucher specimens were deposited at the Agriculture Canada herbarium (DOA) or University of Ottawa herbarium (OTT). A total of 217 quadrats were examined.

### *Soil analysis*

Five soil cores (10 cm depth, 3 cm diameter) were taken from each quadrat sampled as part of the field survey. One core was taken from the center and one from each corner and samples were pooled for each quadrat and frozen within 8 h. Soil samples were then analyzed for four major macronutrients (nitrate, phosphorus, potassium, and magnesium), pH, and percent organic content. Chemical analyses were performed by Agri-Food Laboratories in Guelph, Ontario. Nitrates were extracted in deionized water and assayed with an ion selective electrode; total phosphorus was measured by the sodium bicarbonate extractable method and potassium and magnesium were assayed by ammonium acetate extraction method (McKeague 1978). Percent organic content was calculated from a subsamples mass loss on ignition at 500°C for 12 h.

### *Species position along natural gradients*

A mean species position index provides a simple, comparative measure of the relative distribution of species along discrete gradients in the field and has been used in comparative studies comparing experimentally determined measures of functional species attributes with field distribution (e.g., Wilson and Keddy 1986*b*, McCanny et al. 1990). This method loses some of the information afforded by more complex analysis of species distribution patterns along environmental gradients but is useful for large-scale comparative work.

Species abundance values were used to calculate the mean position of each species along a particular gradient. Only species present in at least five quadrats were examined. The mean position of each species along a specified gradient was calculated as follows:

$$e_i = \frac{\sum a_{ij} b_j}{\sum a_{ij}},$$

where $e_i$ represents the mean position of the $i^{\text{th}}$ species on the specified gradient; $a_{ij}$ represents the abundance of the $i^{\text{th}}$ species in the $j^{\text{th}}$ quadrat and $b_j$ represents the environmental/community measure for that quadrat. The community measures used were standing crop (in grams per 0.25 m$^2$) and soil percent organic content, and environmental measures used were soil nitrate content (milligrams per kilogram), soil phosphorus content (milligrams per kilogram), soil magnesium content (milligrams per kilogram), soil potassium content (milligrams per kilogram), and pH.

### *Competitive performance*

Relative competitive performance was experimentally determined for 44 herbaceous wetland species representing a broad range in life history types from small evergreen rosette species (e.g., *Eriocaulon septangulare*) to large clonal perennials (e.g., *Typha* × *glauca*). A modified additive design was used to assess competitive performance as the relative performance of each species (test species) to suppress the growth of a common indicator species or phytometer (Gaudet and Keddy 1988).

content; N = soil nitrate content; Mg = soil magnesium content. Spearman rank correlation was used on untransformed data.

| K | | Mg | | pH | |
|---|---|---|---|---|---|
| *r* | *P* | *r* | *P* | *r* | *P* |
| 0.58 | $P < 0.00001$ | 0.67 | $P < 0.00001$ | −0.28 | $P < 0.00001$ |
| 0.50 | $P < 0.00001$ | 0.51 | $P < 0.00001$ | −0.47 | $P < 0.00001$ |
| 0.56 | $P < 0.00001$ | 0.66 | $P < 0.00001$ | −0.13 | $P = 0.0662$ |
| 0.53 | $P < 0.00001$ | 0.63 | $P < 0.00001$ | −0.02 | $P = 0.8137$ |
| | | 0.70 | $P < 0.00001$ | −0.28 | $P < 0.00001$ |
| | | | | −0.14 | $P = 0.0291$ |

All 44 species were tested against the phytometer *Lythrum salicaria.* This species was selected because it is an ubiquitous wetland species of moderate size that is easily established as a seedling and grows vigorously to adult size. To test the robustness of the phytometer method, a subset of 10 species were additionally tested against the phytometer *Penthorum sedoides.* To ensure uniformity in size and developmental stage, all phytometers were grown from seed collected at the Luskville study site in September 1985, cleaned and stored at 4°C in sterile, wet sand until March 1986. Seeds were germinated on filter paper, transplanted to a sterile planting medium and grown in a glasshouse at 70°. On 15 April 1986, seedlings, selected for uniformity in size, were transplanted to the center of 1-L pots filled with a sterile, organic potting mix (ProMix) and left to adjust for 1 wk and misted daily.

In April 1986, test species were collected as ramets (vegetative units composed of a single viable shoot) from the study locations described above. Four individuals of each test species were planted in a systematic design around the phytometer. Test species were also planted singly to assess optimal growth under the experimental conditions. Ten representative individuals of each species were selected for determination of initial dry mass. Pots were placed in a randomized block design (five replicates per species) in an outdoor compound and watered daily. A cylinder of fiberglass window screen 30 cm high was installed around each pot on 30 May to ensure that ramets did not influence the growth of plants in other pots. The experiment was harvested during September 1986 just as plants began to senesce as evidenced by yellowing of photosynthetic tissue. Plants were dried to constant mass and the total biomass of the test species and biomass of the phytometer in each pot were measured. Belowground portions were separated and washed prior to drying. Results from the competition experiment were used to determine relative competitive performance. Competitive performance was expressed as the percent reduction in phytometer biomass as follows:

$$\mathrm{CP}_i = \frac{\mathrm{P}_1 - \mathrm{P}_{2i}}{\mathrm{P}_1} \times 100,$$

where $\mathrm{CP}_i$ is the relative competitive ability of the $i^{\text{th}}$ species; $\mathrm{P}_1$ is the biomass of the phytometer grown alone (control) and $\mathrm{P}_{2i}$ is the mass of the phytometer when grown with the $i^{\text{th}}$ species. Results were based on the average value of five replicates per species.

### *Competitive performance and field distribution*

Correlations were calculated between mean position on the nitrogen, phosphorus, magnesium, potassium, percent organic content, pH, and standing crop gradients using Pearson's *r*. Only 40 species were used in this analysis due to a lack of adequate field distribution for four of the species. Statsgrahics (Version 4.0, STSC 1989) and Tablecurve (Version 3.0, Jandel Scientific 1991) statistical software packages were used for all statistical analysis.

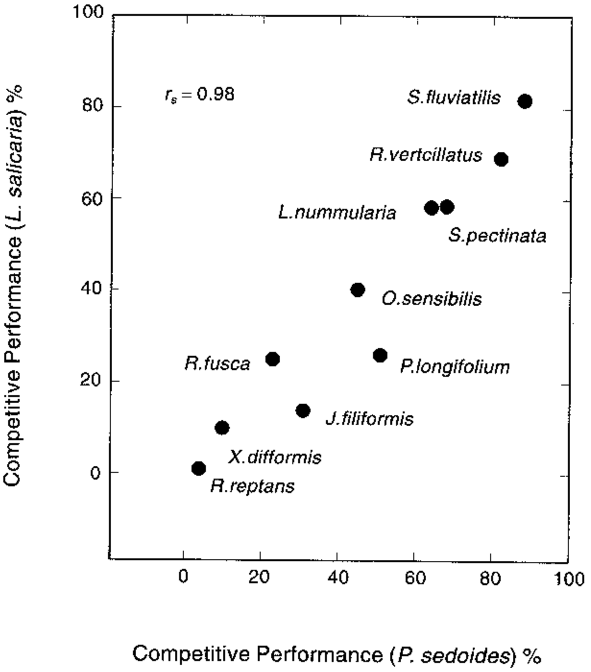

FIG. 1. The relationship between relative competitive performance evaluated using two different phytometers: *Penthorum sedoides* and *Lythrum salicaria* ($r_s = 0.98$; $P < 0.0001$). Competitive performance is based on percent reduction in phytometer biomass when grown with test species ($n = 10$ species; five replicates per species).

TABLE 2. Relative competitive performance expressed as percent reduction in phytometer biomass for 44 herbaceous shoreline plant species (five replicates per species). All species were grown with the phytometer *L. salicaria* in a sterile, high-nutrient organic mix (Promix). A Kruskal-Wallis single-factor analysis of variance by ranks (Zar 1974) showed that there is a significant species effect on percent reduction in phytometer biomass ($H = 171$; $k = 44$; $P < 0.0001$).

| Species | Relative competitive performance (%) | Standard deviation |
|---|---|---|
| *Lythrum salicaria* | 96 | 1.58 |
| *Bidens cernua* | 91 | 5.54 |
| *Phalaris arundinacea* | 89 | 7.02 |
| *Stachys palustris* | 87 | 3.91 |
| *Typha* × *glauca* | 86 | 6.80 |
| *Scirpus fluviatilis* | 82 | 7.09 |
| *Pilea pumila* | 80 | 2.49 |
| *Carex rostrata* | 79 | 3.97 |
| *Lysimachia thyrsiflora* | 77 | 3.83 |
| *Lysimachia ciliata* | 76 | 5.03 |
| *Potentilla anserina* | 72 | 4.82 |
| *Rumex verticillatus* | 69 | 3.39 |
| *Eupatorium maculatum* | 69 | 5.43 |
| *Mentha arvensis* | 67 | 15.17 |
| *Acorus calamus* | 67 | 4.39 |
| *Iris versicolor* | 63 | 9.03 |
| *Hypericum ellipticum* | 62 | 3.11 |
| *Scirpus validus* | 59 | 8.93 |
| *Polygonum hydropiperoides* | 59 | 19.20 |
| *Spartina pectinata* | 59 | 6.99 |
| *Lysimachia nummularia* | 58 | 7.79 |
| *Carex crinita* | 58 | 7.89 |
| *Galium palustre* | 56 | 8.63 |
| *Triadenum fraseri* | 52 | 8.26 |
| *Viola lanceolata* | 51 | 8.38 |
| *Impatiens capensis* | 49 | 12.18 |
| *Leersia oryzoides* | 48 | 5.03 |
| *Lysimachia terrestris* | 44 | 4.32 |
| *Onoclea sensibilis* | 40 | 7.50 |
| *Dulichium arundinaceum* | 37 | 6.80 |
| *Eleocharis erythropoda* | 29 | 11.40 |
| *Panicum longifolium* | 26 | 9.3 |
| *Eriocaulon septangulare* | 25 | 5.40 |
| *Rhyncospora fusca* | 25 | 13.44 |
| *Anenome canadensis* | 23 | 12.66 |
| *Sabatia kennedyana* | 23 | 17.93 |
| *Juncus pelocarpus* | 23 | 2.51 |
| *Drosera intermedia* | 14 | 9.91 |
| *Juncus filiformis* | 14 | 16.68 |
| *Eleocharis palustris* | 13 | 17.35 |
| *Juncus militaris* | 11 | 7.81 |
| *Xyris difformis* | 10 | 4.95 |
| *Lobelia dortmanna* | 4 | 9.31 |
| *Ranunculus reptans* | 1 | 4.09 |

## RESULTS

### *Species distribution*

Species showed a broad range in distribution along the seven gradients measured (Appendix). The mean position of species along the standing crop gradient varied from less than 5 g/0.25 $m^2$ to 285 g/0.25 $m^2$; along the percent organic content gradient from less than 1% to 25%; along the phosphorus gradient from 2.5 to 26.8 ppm; and along the nitrogen gradient from 3.4 to 21 mg/kg.

Standing crop is presumed to integrate community response to a combined gradient of stress and disturbance (Grime 1979, Keddy 1989). Our results show that standing crop is correlated with all of the macronutrient levels but most strongly with soil phosphorus (Table 1). Our results do not enable an exploration of other factors contributing to standing crop.

### *Competitive performance*

Species ranged in their ability to suppress the growth of a common phytometer (*Lythrum salicaria*) from 96% suppression (*Lythrum salicaria*) to 1% suppression (*Ranunculus reptans*) (Table 2). Results using *Penthorum sedoides* as a phytometer were similar and position in the hierarchy was highly correlated irrespective of the phytometer used (Fig. 1). These results suggest that the phytometer method provides a robust measure of relative competitive effect and that the hierarchy established using this method is a reasonable approximation of a more global measure of competitive performance that would have been obtained if all possible pairwise interactions were considered.

### *The relationship between competitive performance and species distribution*

Species competitive performance was significantly correlated with position on each measured environmental gradient (Table 3, Fig. 2). When all seven environmental variables were included, multiple linear regression showed that there was a strong predictive relationship between relative competitive performance of species and their position on the environmental gradient ($R^2 = 0.67$; $P < 0.00001$). However, a single variable, standing crop, could explain most of this vari-

TABLE 3. Correlation ($r$) between relative competitive performance and mean position on each environmental gradient for 40 species of wetland plants. Competitive performance (expressed in terms of percent reduction in phytometer biomass) was arcsine transformed for analysis. All measures of mean position on the environmental gradient were log transformed except for percent organic content, which was arcsine transformed.

| Mean position on environmental gradient | Correlation ($r$) with competitive performance | $P$ |
|---|---|---|
| Standing crop (g/0.25 $m^2$) | 0.81 | <0.00001 |
| Soil nitrate content (mg/kg) | 0.67 | <0.00001 |
| Soil phosphorus content (mg/kg) | 0.70 | <0.00001 |
| Soil magnesium content (mg/kg) | 0.66 | <0.00001 |
| Soil potassium content (mg/kg) | 0.61 | <0.00001 |
| Soil pH | 0.40 | 0.0108 |
| Percent organic content | 0.71 | <0.00001 |

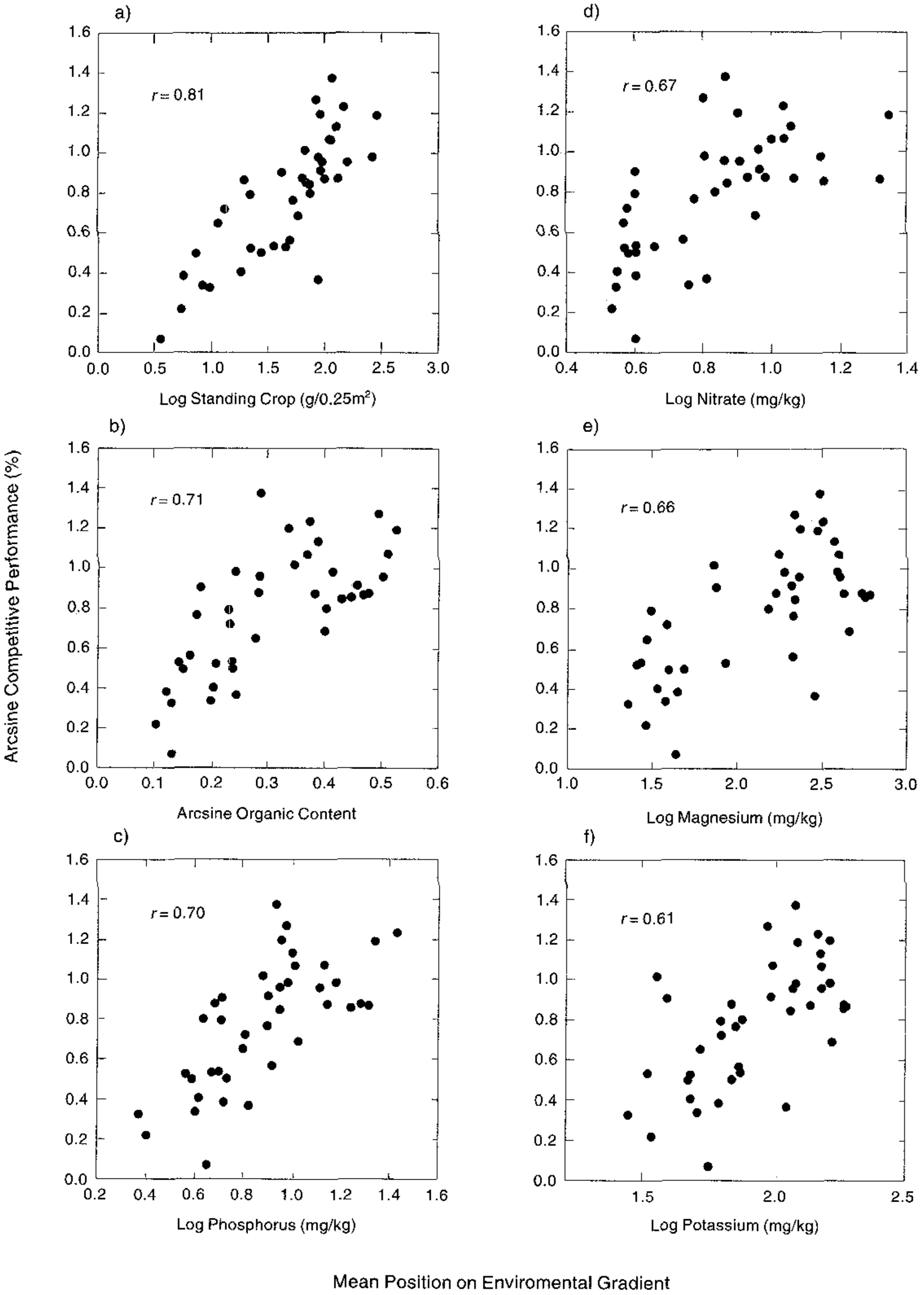

FIG. 2. Relationship between relative competitive performance (percent reduction in phytometer biomass) and position of species ($n = 40$) on the (a) standing crop (g/0.25 m²); (b) percent organic content; (c) soil phosphorus (mg/kg); (d) soil nitrate (mg/kg); (e) soil magnesium (mg/kg); and (f) soil potassium (mg/kg) gradients. For all relationships $P < 0.00001$. Competitive performance is expressed as percent reduction in the biomass of the phytometer *Lythrum salicaria*.

TABLE 4. Correlation ($r$) between relative competitive performance and mean position on each environmental gradient for monocotyledon species only ($n = 20$) and dicotyledon species only ($n = 20$).

| Mean position on environmental gradient | Correlation ($r$) with competitive performance | | | |
|---|---|---|---|---|
| | Monocot | | Dicot | |
| | $r$ | $P$ | $r$ | $P$ |
| Standing crop (g/0.25 $m^2$) | 0.84 | $P < 0.00001$ | 0.82 | $P < 0.00001$ |
| Soil phosphorus content (mg/kg) | 0.86 | $P < 0.00001$ | 0.41 | $P = 0.07$ |
| Soil nitrate content (mg/kg) | 0.85 | $P < 0.00001$ | 0.54 | $P = 0.01$ |
| Soil pH | 0.27 | $P = 0.24$ | 0.53 | $P = 0.02$ |
| Soil potassium content (mg/kg) | 0.76 | $P < 0.00001$ | 0.50 | $P = 0.02$ |
| Soil magnesium content (mg/kg) | 0.74 | $P < 0.00001$ | 0.63 | $P = 0.003$ |
| Percent organic content | 0.85 | $P < 0.00001$ | 0.60 | $P = 0.006$ |

ation ($R^2 = 0.64$; $P < 0.00001$), whereas all of the fertility measures combined explained <55% of the variation.

The shoreline plants used in this study included an equal number of monocotyledons and dicotyledons from along the environmental gradient. When these two major taxonomic groups were treated as separate data subsets, the relationship between position on the environmental gradient and competitive performance was much stronger for monocotyledons than for dicotyledons (Table 4). Though both monocotyledons and dicotyledons showed a strong relationship between competitive performance and position on the standing crop gradient, the two taxonomic groups showed different responses when macronutrients were considered. Monocotyledons showed a strong relationship between competitive performance and position on the percent organic content, phosphorus, nitrate, potassium, and magnesium gradients. Dicotyledons, in contrast, were not significantly correlated with position on the macronutrient gradients.

## DISCUSSION

### *Relative competitive performance*

Results of the comparative screening of species shows that the 44 wetland species in this study can be ranked in a competitive hierarchy with tall, leafy species (e.g., *Typha × glauca, Scirpus fluviatilis*) at the top of the hierarchy and small isoetid species (e.g., *Eriocaulon septangulare, Lobelia dortmanna*) at the bottom of the hierarchy. This ranking conforms to Grime's (1977, 1979) proposed characteristics of competitive dominants which are generally indicative of an ability to capture resources, especially to pre-empt light and space. It appears that many plant and animal communities have competitive hierarchies (Goldsmith 1978, Gilpin et al. 1986, Mitchley and Grubb 1986, Wilson and Keddy 1986*b*, Tilman and Wedin 1991). Keddy and Shipley (1989) found highly significant hierarchies in published competition matrices from seven different plant communities including lakeshores, seacliffs, and chalk grassland. However, the small number of species involved makes it difficult to draw generalizations about pattern or mechanism in natural communities. The experimentally derived hierarchy in this study provides a systematic measure of competitive performance for a large number of species and a general tool for exploring the relationship between competitive ability, environmental gradients, and coarse-scale community pattern.

Many factors may influence a species' ranking within a competitive hierarchy (Harper 1977, Fowler 1982, Gilpin et al. 1986). This experiment was conducted under conditions considered to be most representative of the highly productive conditions of wetlands and those in which competition is presumably most important (Grime 1979, Wilson and Keddy 1986*a*). Our results do not exclude the possibility that the hierarchy changes with varying environmental conditions (Tilman 1985), although recent work, comparing several species with a broad range in realized distribution along natural resource gradients, shows that resource availability does not significantly affect the relative competitive performance of species (e.g., Campbell and Grime 1992, Gaudet 1993).

There are some limitations to the experimental approach used to measure competitive performance in this study. Recently, Grace et al. (1992) have experimentally explored Connolly's (1986) suggestion of size bias in competition experiments, concluding that measures based on relative yield were correlated with initial size of plants over at least 2 yr. The importance of initial plant size cannot be clearly separated in the current experiment, which was run over only 1 yr. Also, though this study provides a direct measure of competitive performance across a range of species, a single starting density was used that may not reflect the actual density at which species interact in the field. Starting density was held constant to enable a systematic screening of the relative competitive ability of a large number of species. Though there is no conclusive evidence as to the effect different planting densities may have had on these results, our results were comparable to those using different starting densities (Gaudet 1993, Wilson and Keddy 1986*b*). It may be that results would have varied if this experiment had been conducted over a longer period of time. However, this time period was clearly adequate to detect differential response in competitive performance. Whether the hierarchy would have shifted significantly in subsequent years is unclear and may be an important direction for future studies. The experimental conditions may also have limited the contribution of such factors as lateral spread to relative competitive performance. Under the experimental conditions of this study, annual species such as *Bidens cernua* exhibited a high relative degree of competitive performance. In field situations, the capacity for extensive lateral spread and pre-exemption of space by long-lived perennial species such as *Typha* sp. may strongly influence dominance (e.g., Grace and Wetzel 1981, Day et al. 1988). While subject to recognized limitations, this experiment does allow, as do traditional competitive experiments, among-species comparisons of competitive performance while controlling for density, abiotic factors, and neighbors (McGilchrist 1965, Harper 1977, Fowler 1982).

### *Competitive performance and field distribution*

Though plant ecologists have assumed competition is a predominant factor in determining community structure (e.g., Grime 1979, Tilman 1988, Austin 1990), there are few tests that directly test the importance of competition as a determinant of coarse-scale community pattern. Previous work has described the role of competition in producing zonation patterns (e.g., Connell 1961, Austin and Austin 1980, Lubchenco 1980). Vegetation theory suggests the importance of competition but cannot provide causal answers (Ellenberg and Mueller-Dombois 1974, Austin 1990). Inferences about the relationship between competitive performance and field distribution have been drawn from studies that have measured species characteristics possibly related to competitive success such as maximum potential growth rate (Grime and Hunt 1975, Boorman 1982) or height (Menges and Waller 1983). However, there is no conclusive evidence that these traits actually confer improved competitive performance at the general scale at which they were examined in the field. Growth rate, for example, may relate to both ruderal (sensu Grime 1979) and competitive strategies. More recently, Wilson and Keddy (1986*b*) have directly shown that competitive performance varies predictably with soil percent organic content gradient. The generality of this relationship had not previously been tested across a large range of species or compared across distinct environmental resource and community gradients examined here. Our results clearly show that species distributions along natural resource gradients are related to their relative competitive performance such that species with high competitive performance occur in nutrient-rich (fertile) areas and species with low competitive performance occur in low-nutrient (infertile) areas.

We have taken a very simple univariate approach to testing the prediction that competitive ability varies predictably along resource gradients and have shown the importance of this relationship along distinct macronutrient gradients. Austin and Smith (1989) emphasize that complex patterns of community response may emerge when several different environmental gradients are considered simultaneously and that comparative information on the position in the environmental space defined by resources, disturbance, and direct variables is necessary to testing and building plant community theory. Our study was not intended to explore such complex interrelationships or to provide mechanistic interpretations of pattern, but as a simple test of the general relationship between competitive performance and distribution along specified gradients at a broad scale. However, the strong relationship between standing crop and competitive performance is noteworthy in the context of Austin and Smith's (1989) argument. Standing crop is a complex emergent community property embodying the response to interacting environmental gradients in a single measure. This may explain why standing crop is emerging as a key state variable in community ecology (e.g., Grime 1973, 1979, Wheeler and Giller 1982, Wilson and Keddy 1986*a*, Day et al. 1988, Moore et al. 1989, Reader and Best 1989, Reader et al. 1994) in that it defines just that "position in environmental space defined by disturbance, resources and direct variables." Our results add to the growing literature on the importance of standing crop in the development of predictive community ecology, a stated goal of which is to predict complex things that are difficult to measure (such as competitive ability) from simple measurable things (such as standing crop) (Peters 1982).

The relationship between competitive performance and field distribution is significant even given the expected sampling variability in results from such a broad range of sites and the simple screening techniques used to measure relative competitive performance and field distribution. This suggests that the relationship between competitive performance and pattern in the field is an important and pervasive feature of natural shoreline plant communities. How these results would have varied using hierarchies established under different resource availability, or other environmental conditions, is not known (but see Keddy et al. 1994). Considerable variability remains in the relationship between our measure of competitive performance and field distribution. It must be emphasized that species relative competitive performance is unlikely to be the only determinant of pattern along the shoreline gradients examined here, and it is clearly not expected that all, or even most, of the variation can be explained by this single measure. Explaining the residual variation along the gradient is an important goal for future research. In the development of general predictive community theory, it is likely that several functional attributes of plants, such as measures of competitive ability, growth rate, and stress tolerance, as well as other environmental gradients, will be important.

The different results for monocotyledons and dicotyledons are also noteworthy in that they indicate that interpretation may vary if the data is examined in terms of "functional groups" (Southwood 1988, Keddy 1990*a*). Monocotyledons may have evolved more mechanical and physiological resistance to wave exposure and flooding, common types of disturbance in shoreline communities (Grace and Wetzel 1982, Menges and Waller 1983). Therefore, though both groups of species vary predictably along the standing crop gradient (presumably a combined gradient of stress and disturbance); the variation in monocotyledon distribution may be explained by fertility gradients. The distribution of dicotyledons on the other hand, may be more affected by the disturbance component of the gradient. Though results are not conclusive, the contrasting architecture of these two groups (for example, monocotyledons have meristems buried even during peak growth, whereas dicotyledons expose them at the top of the stem), suggests that dicotyledons may respond to disturbance much differently than monocotyledons. Given that major studies on shoreline plant communities have concluded that disturbance is a major determinant of pattern (e.g., Day et al. 1988, Moore 1990), an examination of this general conclusion with reference to these two functionally, as well as taxonomically, distinct groups is warranted.

Despite controversy that may surround this novel approach to measuring competitive ability (and all approaches were at one time novel), it is important to note that this simple, "crude" measure of relative competitive performance appears to have broad implications for understanding the distribution of shoreline plant species along natural gradients of fertility and standing crop. Whether similar results can be found in other communities at this scale remains to be explored. However, we emphasize that in exploring and reconciling competing views about the role and nature of competition and of the appropriate ways to measure it, the scale at which one asks, and answers, questions is of paramount importance. Rather than representing competing views, measures and results may simply represent work at different scales. Reconciling the different scales of study in developing a general framework for understanding competition at the community level is perhaps one of the most important challenges in community ecology today. Use of a comparative approach as described here is relatively novel, but is amenable to addressing questions at the broad, multispecies scale. Whether other approaches provide a more useful estimate of competitive performance, with broad predictive power at this general scale of community organization, remains to be examined. The simplified phytometer approach, though sacrificing the detailed results of experiments based on pairwise interactions, does enable a systematic exploration of the competitive performance of a large number of species under standardized conditions; in this sense there are few alternative approaches available for studies asking these general questions.

## ACKNOWLEDGMENTS

We thank D. Brunton, P. Catling, D. Currie, J. Grace, D. Moore, S. Warwick, E. Weiher, S. Wilson, and I. Wisheu for their advice and other assistance. This work was supported by an NSERC scholarship to C. Gaudet and an NSERC operating grant to P. Keddy.

## LITERATURE CITED

Allen, T. F. H. 1987. Hierarchical complexity in ecology: a noneuclidean conception of the data space. Vegetatio **69**:17–25.

Austin, M. P. 1986. The theoretical basis of vegetation science. Trends in Ecology and Evolution **1**:161–164.

Austin, M. P., and B. O. Austin. 1980. Behaviour of experimental plant communities along a nutrient gradient. Journal of Ecology **68**:891–918.

Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. Vegetatio **83**:35–48.

Boorman, L. A. 1982. Some plant growth patterns in relation to the sand dune habitat. Journal of Ecology **70**: 607–614.

Campbell, B. D., and J. M. Grime. 1992. An experimental test of plant strategy theory. Ecology **73**:15–29.

Clements, F. E. 1933. Competition in plant societies. News Service Bulletin, Carnegie Institution of Washington, 2 April 1933.

Connell, J. H. 1961. The influence of interspecific competition and other factors in the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710–723.

———. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist **122**:662–696.

Canaille, J. 1986. On difficulties with replacement-series methodology in mixture experiments. Journal of Applied Ecology **23**:125–137.

Day, R. T., P. A. Keddy, J. McNeill, and T. Carleton. 1988. Fertility and disturbance gradients: a summary model for riverine marsh vegetation. Ecology **69**:1044–1054.

de Wit, C. T. 1960. On competition. Verslagen van Landbouwkundige Onderzoekingen **66**:1–82.

Ellenberg, H. 1988. Floristic changes due to nitrogen deposition in Central Europe. *In* J. Nilsson and P. Greenfelt, editors. Critical loads for sulphur and nitrogen. Report from a workshop held in Stokloster, Sweden, 19–24 March. Nordic Council of Ministers, Copenhagen.

Ellenberg, H., and D. Mueller-Dombois. 1974. Aims and methods of vegetation study. Wiley, New York, New York, USA.

Fowler, N. 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. Journal of Ecology **70**:77–92.

Gaudet, C. L. 1993. Competition in shoreline plant communities: a comparative approach. Dissertation. University of Ottawa, Ottawa, Ontario, Canada.

Gaudet, C. L., and P. A. Keddy. 1988. A comparative approach to predicting competitive ability from plant traits. Nature **334**:242–243.

Gilpin, M. E., M. P. Carpenter, and M. J. Pomerantz. 1986. The assembly of a laboratory community: multispecies competition in *Drosophila*. Pages 23–40 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. American Naturalist **139**:771–801.

Goldsmith, F. B. 1978. Interaction (competition) studies as a step towards the synthesis of seacliff vegetation. Journal of Ecology **66**:921–931.

Goldsmith F. B., and C. M. Harrison. 1976. Description and analysis of vegetation. Pages 85–164 *in* S. B. Chapman, editor. Methods in plant ecology. Blackwell Scientific, London, England.

Grace, J. B., J. Keough, and G. R. Guntenspergen. 1992. Size bias in traditional analyses of substitutive competition experiments. Oecologia **90**:429–434.

Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental fields studies. American Naturalist **118**:463–474.

Grace, J. B., and R. G. Wetzel. 1982. Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. Canadian Journal of Botany **60**: 46–57.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature **250**:26–31.

———. 1979. Plant strategies and vegetation processes. John Wiley, Chichester, England.

———. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecolgical and evolutionary theory. American Naturalist **111**:1169–1194.

Grime, J. P., and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in local flora. Journal of Ecology **63**:393–422.

Harper, J. L. 1977. Population biology of plants. Academic, London, England.

Keddy, P. A. 1981. Vegetation with Atlantic coastal plain affinities in Axe Lake near Georgian Bay, Ontario. Canadian Field Naturalist **95**:241–248.

———. 1983. Shoreline vegetation in Axe Lake, Ontario. Effects of exposure on zonation patterns. Ecology **64**: 331–344.

———. 1984. Wave disturbance on lakeshores and the within-lake distribution of Ontario's Atlantic coastal plain flora. Canadian Journal of Botany **63**:656–660.

———. 1989. Competition. Chapman and Hall, London, England.

———. 1990*a*. The use of functional as opposed to phylogenetic systematics: a first step in predictive community ecology. Pages 387–406 *in* S. Kawano, editor. Biological approaches and evolutionary trends in plants. Harcourt Brace Jovanovich, London, England.

———. 1990*b*. Competitive hierarchies and centrifugal organization in plant communities. Pages 265–290 *in* J. B. Grace and D. Tilman, editors. Perspectives in plant competition. Academic Press, New York, New York, USA.

———. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science **3**:157–164.

Keddy, P. A., and P. MacLellan. 1991. Centrifugal organization in forests. Oikos **59**:75–84.

Keddy, P. A., and B. Shipley. 1989 Competitive hierarchies in plant communities. Oikos **54**:234–241.

Keddy, P. A., L. Twolan-Strutt, and I. C. Wisheu. 1994. Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? Journal of Ecology **82**:635–643.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology **61**:333–344.

McCanny, S. J., P. A. Keddy, T. J. Arnason, C. L. Gaudet, D. R. J. Moore, and B. Shipley. 1990. Fertility and the food quality of wetland plants: a test of the resource availability hypothesis. Oikos **59**:373–381.

McGilchrist, C. A. 1965. Analysis of competition experiments. Biometrics **21**:975–985.

McKeague, J., editor. 1978. Manual on soil sampling and methods of analysis. Canadian Society of Soil Science, Ottawa, Ontario, Canada.

Menges, E. S., and D. M. Waller. 1983 Plant strategies in relation to elevation and light in floodplain herbs. American Naturalist **122**:454–473.

Mitchley, J., and P. J. Grubb. 1986. Control of relative abundance of perennials in chalk grassland in southern England. I. Constancy of rank order and results of pot-and-field experiments on the role of interference. Journal of Ecology **74**:1139–1166.

Moore, D. R. J. 1990. Pattern and process in wetlands of varying standing crop: the importance of scale. Dissertation. University of Ottawa, Ottawa, Ontario, Canada.

Moore, D. R. J., P. A. Keddy, C. L. Gaudet, and I. C. Wisheu. 1989. Conservation of wetlands: do infertile wetlands deserve a higher priority. Biological Conservation **47**:203–217.

Moore, D. R. J., and P. A. Keddy. 1989. The relationship between species richness and standing crop in wetlands: the importance of scale. Vegetatio **79**:99–106.

O'Neill, R. V., D. L., DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Reader, R. J., and B. J. Best. 1989. Variation in competition along an environmental gradient: *Hieracium floribundum* in an abandoned pasture. Journal of Ecology **77**:673–684.

Reader, R. J., and T. R. E. Southwood. 1981. The relationship between palatability to invertebrates and the successional status of a plant. Oecologia (Berlin) **51**:271–275.

Reader, R. J., et al. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. Ecology **75**:1753–1760.

Shipley, B., P. A. Keddy, and L. P. Lefkovitch. 1991. Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. Canadian Journal of Botany **69**:1420–1424.

Snow, A. A., and S. W. Vince. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. Journal of Ecology **72**:669–684.

Southwood, T. R. E. 1988. Tactics, strategies and templets. Oikos **52**:3–18.

Statgraphics. 1989. Statistical graphics system, version 4. STSC, Rockville, Maryland, USA.

TableCurve. 1991. Curve fitting software, version 3.0. Jandel Scientific, Corte Madera, California, USA.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

———. 1985. The resource ratio hypothesis of plant succession. American Naturalist **125**:827–852.

———. 1988. Plant strategies and the structure and dynamics of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D., and D. Wedin. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology **72**:685–700.

Turkington, R., E. Klein, and C. P. Chanway. 1993. Interactive effects of nutrients and disturbance: an experimental test of plant strategy theory. Ecology **74**:863–878.

Welbank, P. J. 1963. A comparison of the competitive effects of some common weed species. Annals of Applied Biology **51**:107–125.

Wheeler, B. D., and K. E. Giller. 1982. Species richness in grassland and wetland communities. Vegetatio **53**:121–126.

Wilson, S. D., and P. A. Keddy. 1985. Plant zonation on a shoreline gradient: physiological response curves of component species. Journal of Ecology **73**:851–860.

Wilson, S. D., and P. A. Keddy. 1986*a*. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. American Naturalist **127**: 862–869.

Wilson, S. D., and P. A. Keddy. 1986*b*. Species competitive ability and position along a natural stress/disturbance gradient. Ecology **67**:1236–1242.

Wilson, S. D., and J. M. Shay. 1990. Competition, fire and nutrients in a mixed-grass prairie. Ecology **71**:1959–1967.

Wilson, S. D., and D. Tilman. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. Oecologia (Berlin) **88**:61–71.

Wisheu, I. C. 1987. Species richness-standing crop relationships on an infertile shoreline in Nova Scotia. Thesis. University of Ottawa, Ottawa, Ontario, Canada.

Wisheu, I. C., and P. A. Keddy. 1989. The conservation and management of a threatened coastal plain plant community in eastern North America (Nova Scotia, Canada). Biological Conservation **48**:229–238.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

## APPENDIX

Mean position of 40 wetland species along the following environmental gradients: standing crop (SC), soil percent organic content (Org), soil phosphorus content (P), soil nitrate content (N), soil pH (pH), soil magnesium content (Mg), and soil potassium content (K). Species position was weighted by frequency of occurrence within each quadrat. The number of quadrat subdivisions in which a species occurred is indicated (*n*). Unless indicated by an *, species occurred in at least five 0.25-$m^2$ quadrats.

| Species | *n* | Statistics | SC ($g/0.25\ m^2$) | Org (%) | P (mg/kg) | N (mg/kg) | K (mg/kg) | pH | Mg (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|
| *Acorus calamus* | 15 | $\bar{X}$ | 158.23 | 23.06 | 12.93 | 8.13 | 117.27 | 5.93 | 399.00 |
| | | SE | 8.11 | 2.69 | 1.68 | 0.57 | 15.35 | 0.14 | 34.59 |
| *Bidens cernua* | 93 | $\bar{X}$ | 83.6 | 22.58 | 9.43 | 6.34 | 93.42 | 6.64 | 220.67 |
| | | SE | 4.92 | 2.60 | 0.42 | 0.26 | 3.73 | 0.14 | 9.67 |
| *Carex crinita* | 24 | $\bar{X}$ | 68.91 | 18.55 | 17.29 | 14.33 | 183.58 | 6.4 | 565.10 |
| | | SE | 6.26 | 0.85 | 0.74 | 0.68 | 2.08 | 0.02 | 5.93 |
| *Carex rostrata* | 13 | $\bar{X}$ | 109.63 | 23.99 | 13.46 | 10.92 | 97.92 | 6.62 | 178.54 |
| | | SE | 19.96 | 2.15 | 0.92 | 3.30 | 6.2 | 0.14 | 16.78 |
| *Drosera intermedia* | 60 | $\bar{X}$ | 18.22 | 4.14 | 4.13 | 3.53 | 47.97 | 5.62 | 34.08 |
| | | SE | 1.66 | 0.61 | 0.28 | 0.11 | 3.44 | 0.05 | 2.37 |
| *Dulichium arundinaceum* | 17 | $\bar{X}$ | 11.67 | 7.57 | 6.29 | 3.71 | 52.29 | 5.27 | 29.29 |
| | | SE | 1.39 | 0.92 | 0.47 | 0.28 | 4.71 | 0.05 | 1.76 |
| *Eleocharis erythropoda* | 247 | $\bar{X}$ | 48.89 | 2.63 | 8.25 | 5.51 | 73.28 | 7.45 | 212.47 |
| | | SE | 1.71 | 0.12 | 0.11 | 0.13 | 1.94 | 0.05 | 4.56 |
| *Eleocharis palustris* | 219 | $\bar{X}$ | 87.09 | 5.88 | 6.56 | 6.48 | 111.28 | 6.38 | 286.66 |
| | | SE | 2.37 | 0.26 | 0.14 | 0.25 | 3.18 | 0.04 | 7.99 |
| *Eriocaulon septangulare* | 72 | $\bar{X}$ | 44.91 | 2.03 | 4.67 | 4.53 | 32.68 | 6.73 | 85.96 |
| | | SE | 4.02 | 0.09 | 0.22 | 0.65 | 1.06 | 0.09 | 5.57 |
| *Eupatorium maculatum* | 19 | $\bar{X}$ | 88.36 | 5.74 | 9.58 | 6.42 | 120.32 | 7.06 | 188.32 |
| | | SE | 10.33 | 0.90 | 0.39 | 0.66 | 15.13 | 0.13 | 11.73 |
| *Galium palustre* | 15 | $\bar{X}$ | 74.16 | 17.29 | 8.87 | 7.47 | 114.87 | 6.67 | 217.47 |
| | | SE | 5.23 | 1.96 | 0.62 | 0.49 | 2.07 | 0.09 | 13.31 |
| *Hypericum ellipticum* | 28 | $\bar{X}$ | 42.25 | 3.23 | 5.14 | 4.00 | 38.82 | 6.34 | 75.39 |
| | | SE | 7.3 | 0.55 | 0.37 | 0.18 | 2.08 | 0.21 | 10.20 |
| *Iris versicolor* | 21 | $\bar{X}$ | 92.6 | 19.38 | 7.95 | 9.29 | 96.57 | 6.9 | 207.76 |
| | | SE | 9.8 | 3.4 | 1.5 | 1.73 | 12.06 | 0.17 | 39.41 |
| *Juncus filiformis* | 16 | $\bar{X}$ | 5.67 | 1.46 | 5.25 | 4.00 | 61.5 | 6.47 | 44.87 |
| | | SE | 1.13 | 0.29 | 0.17 | 0.12 | 2.46 | 0.15 | 1.82 |
| *Juncus militaris* | 15 | $\bar{X}$ | 8.35 | 3.95 | 4.00 | 5.73 | 51.14 | 5.4 | 38.27 |
| | | SE | 0.38 | 0.69 | 0 | 0.18 | 1.47 | 0.0 | 4.62 |
| *Juncus pelocarpus* | 70 | $\bar{X}$ | 7.24 | 2.26 | 3.86 | 3.8 | 46.86 | 5.98 | 39.73 |
| | | SE | 1.04 | 0.18 | 0.23 | 0.07 | 2.93 | 0.06 | 1.74 |
| *Leersia oryzoides* | 308 | $\bar{X}$ | 53.37 | 2.99 | 7.9 | 5.99 | 71.28 | 7.4 | 213.12 |
| | | SE | 2.25 | 0.20 | 0.12 | 0.15 | 1.80 | 0.05 | 4.62 |
| *Lobelia dortmanna* | 27 | $\bar{X}$ | 5.42 | 1.06 | 2.52 | 3.41 | 33.89 | 5.8 | 29.19 |
| | | SE | 0.75 | 0.12 | 0.20 | 0.18 | 2.52 | 0.03 | 2.13 |
| *Lysimachia nummularia* | 18 | $\bar{X}$ | 19.77 | 20.25 | 20.5 | 21.00 | 187.5 | 6.4 | 600.00 |
| | | SE | 0.95 | 1.32 | 1.09 | 1.69 | 2.3 | 0.04 | 0.01 |
| *Lysimachia terrestris* | 24 | $\bar{X}$ | 13.31 | 5.34 | 6.42 | 3.8 | 62.79 | 5.67 | 38.58 |
| | | SE | 2.64 | 1.02 | 1.15 | 0.11 | 3.71 | 0.15 | 3.08 |
| *Lysimachia thyrsiflora* | 84 | $\bar{X}$ | 113.22 | 13.11 | 10.25 | 10.05 | 150.66 | 7.73 | 399.86 |
| | | SE | 4.95 | 0.46 | 0.45 | 0.48 | 2.18 | 0.03 | 7.58 |
| *Lythrum salicaria* | 245 | $\bar{X}$ | 114.86 | 8.08 | 8.55 | 7.34 | 119.67 | 6.5 | 310.16 |
| | | SE | 6.08 | 0.36 | 0.25 | 0.25 | 2.79 | 0.08 | 12.71 |
| *Mentha arvensis* | 9 | $\bar{X}$ | 95.34 | 7.89 | 8.88 | 7.33 | 151.11 | 6.88 | 229.11 |
| | | SE | 5.85 | 0.61 | 0.42 | 0.58 | 8.15 | 0.16 | 1.82 |
| *Onoclea sensibilis* | 28 | $\bar{X}$ | 59.31 | 15.18 | 10.61 | 9.07 | 165.79 | 6.44 | 456.68 |
| | | SE | 6.17 | 2.57 | 0.98 | 0.65 | 5.5 | 0.03 | 25.12 |

**APPENDIX.** Continued.

| Species | $n$ | Statistics | SC (g/0.25 m$^2$) | Org (%) | P (mg/kg) | N (mg/kg) | K (mg/kg) | pH | Mg (mg/kg) |
|---|---|---|---|---|---|---|---|---|---|
| *Panicum longifolium* | 17 | $\bar{X}$ | 35.25 | 5.54 | 5.0 | 4.0 | 74.24 | 5.03 | 27.12 |
| | | SE | 2.98 | 0.51 | 0.0 | 0.0 | 1.21 | 0.16 | 1.45 |
| *Phalaris arundinacea* | 69 | $\bar{X}$ | 145.18 | 13.41 | 26.8 | 10.87 | 145.87 | 6.1 | 324.39 |
| | | SE | 6.00 | 0.41 | 4.95 | 0.48 | 5.32 | 0.09 | 12.19 |
| *Polygonum hydropiperoides** | 6 | $\bar{X}$ | 131.80 | 21.01 | 19.00 | 9.67 | 183.67 | 6.28 | 540.50 |
| | | SE | 18.9 | 0.76 | 1.41 | 0.33 | 4.48 | 0.03 | 9.62 |
| *Potentilla anserina* | 130 | $\bar{X}$ | 67.29 | 11.5 | 7.55 | 9.22 | 35.4 | 7.78 | 72.81 |
| | | SE | 1.62 | 0.39 | 0.21 | 0.38 | 0.87 | 0.01 | 1.90 |
| *Ranunculus reptans* | 50 | $\bar{X}$ | 3.55 | 1.71 | 4.48 | 4.0 | 56.3 | 6.26 | 43.88 |
| | | SE | 0.25 | 0.11 | 0.19 | 0.0 | 1.9 | 0.08 | 1.04 |
| *Rhyncospora fusca* | 72 | $\bar{X}$ | 22.21 | 4.3 | 3.64 | 3.70 | 47.93 | 5.44 | 25.59 |
| | | SE | 1.75 | 0.43 | 0.18 | 0.08 | 2.89 | 0.06 | 1.25 |
| *Rumex verticillatus* | 68 | $\bar{X}$ | 261.76 | 16.1 | 15.06 | 14.00 | 162.69 | 5.6 | 384.9 |
| | | SE | 5.89 | 0.23 | 0.24 | 1.16 | 4.39 | 0.03 | 3.91 |
| *Sabatia kennedyana* | 42 | $\bar{X}$ | 27.4 | 5.6 | 5.4 | 4.0 | 69.14 | 5.6 | 49 |
| | | SE | 2.65 | 0.75 | 0.24 | 0.0 | 2.46 | 0.09 | 1.93 |
| *Scirpus fluviatilis* | 103 | $\bar{X}$ | 126.22 | 14.44 | 9.99 | 11.45 | 149.26 | 5.5 | 377.29 |
| | | SE | 2.98 | 0.18 | 0.26 | 0.40 | 1.67 | 0.02 | 5.33 |
| *Scirpus validus* | 484 | $\bar{X}$ | 64.07 | 7.81 | 4.8 | 8.58 | 68.60 | 7.32 | 168.38 |
| | | SE | 1.77 | 0.47 | 0.14 | 0.33 | 2.17 | 0.04 | 5.61 |
| *Spartina pectinata* | 48 | $\bar{X}$ | 100.77 | 13.92 | 13.9 | 11.71 | 137.13 | 6.6 | 422.08 |
| | | SE | 8.65 | 1.18 | 0.85 | 0.80 | 8.98 | 0.08 | 26.72 |
| *Stachys palustris** | 7 | $\bar{X}$ | 90.9 | 11.02 | 9.00 | 8.00 | 162.11 | 7.7 | 237.95 |
| | | SE | 4.34 | 0.96 | 0.04 | 0.00 | 3.41 | 0.09 | 22.90 |
| *Triadenum fraseri* | 90 | $\bar{X}$ | 75.46 | 15.33 | 3.4 | 6.90 | 75.46 | 6.9 | 152.06 |
| | | SE | 4.64 | 1.4 | 0.29 | 0.44 | 5.03 | 0.09 | 13.35 |
| *Typha* × *glauca* | 222 | $\bar{X}$ | 285.29 | 25.29 | 21.76 | 22.23 | 121.85 | 6.8 | 301.00 |
| | | SE | 5.90 | 0.70 | 0.69 | 0.69 | 3.13 | 0.07 | 5.44 |
| *Viola lanceolata* | 44 | $\bar{X}$ | 22.39 | 5.22 | 5.11 | 4.0 | 62.43 | 5.42 | 31.00 |
| | | SE | 2.25 | 0.52 | 0.13 | 0.0 | 1.76 | 0.11 | 1.14 |
| *Xyris difformis* | 32 | $\bar{X}$ | 9.65 | 1.69 | 2.34 | 3.5 | 27.47 | 5.88 | 22.84 |
| | | SE | 1.4 | 0.49 | 0.19 | 0.16 | 2.81 | 0.07 | 1.29 |