

Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants

PAUL KEDDY*, CONNIE GAUDET† and LAUHLAN H. FRASER‡

Department of Biology, University of Ottawa, Ottawa, Ontario, K1N 6N5 Canada

Summary

1 We tested the hypothesis that competitive hierarchies are invariant with respect to changing nutrient supply.

2 The competitive performance of 26 shoreline plant species was determined experimentally as the relative ability to suppress the growth of a common indicator (phytometer) species, *Penthorum sedoides*. Each species was grown with the phytometer under each of two nutrient treatments created with different concentrations of a modified Hoagland's solution ($n = 5$ replicates per species/treatment), for two growing seasons.

3 Although shifts in ranking of relative competitive performance were apparent between nutrient levels, competitive performance under high and low nutrient conditions was significantly correlated in both year 1 ($r = 0.65$) and year 2 ($r = 0.76$), when all species were considered.

4 At the broad community scale, the outcome of competitive interactions thus appears to be relatively predictable and independent of the environment, and therefore provides a useful tool for exploring and understanding community pattern. These results cannot address questions related to the outcome of competitive interactions between similar species or the effects of fine-scale pattern.

Key-words: asymmetric competition, community organization, indicator, phytometer

Journal of Ecology (2000) **88**, 413–423

Introduction

Most pair-wise competitive interactions amongst plants are asymmetric (as reviewed by Shipley 1993; Shipley & Keddy 1994). When two plants are grown both together and separately, the average decrease in performance of each plant due to the other can be compared to give a quantitative estimate of this asymmetry. In most cases, one of the two plants suffers disproportionately. Although many of the published studies address intraspecific competition, such results have also been found in interspecific experiments (Shipley 1993; Shipley & Keddy 1994).

*Present address: Edward G. Shlieder Endowed Chair, Biological Sciences, South-eastern Louisiana University, Hammond, LA 70402, USA.

†Present address: Environment Canada, 7th Floor, Place Vincent Massey, 351 St Joseph Blvd, Hull, Quebec K1A 0H3, Canada.

‡Present address and correspondence: Dr L.H. Fraser, Department of Biology, University of Akron, Akron, OH 44325–3908, USA.

There is evidence to suggest that the degree of asymmetry may be related to the environment, and in particular to habitat productivity. Keddy *et al.* (1997) measured the interspecific competitive asymmetry of 18 species of herbaceous wetland plants on a phytometer at three different soil fertility levels (low, medium and high). They found that the degree of asymmetry (difference of phytometer grown alone and grown with one of the 18 neighbouring species) increased 1.31 times from low to medium, and 1.45 times from low to high. Silvertown *et al.* (1994) found an increased dominance of grasses over non-grasses with increasing rainfall in the Park Grass experiment, which they related to an increase in asymmetric competition between these two groups of plants. Rainfall was positively related with productivity, suggesting that here too the intensity of asymmetric competition increased with increasing productivity.

The asymmetry of competition between species can be extended to the community level by measuring competitive performance for a number of different species. As a general rule, there are plant species

that tend to suppress most of the other plant species they encounter and others that are suppressed by most other species encountered, leading to a ranking from dominant to subordinate. The existence of such competitive hierarchies has been demonstrated in many different plant communities, including sea-cliff (Goldsmith 1978), wetland (Wilson & Keddy 1986a; Johansson & Keddy 1991), chalk grassland (Mitchley & Grubb 1986), weed (Williams 1962) and crop (Harper 1977). The quantitative differences in competitive performance reflected in such hierarchies suggest a general way in which entire communities can be structured by competition (Gaudet & Keddy 1988, 1995).

There are conflicting views as to whether competitive hierarchies remain consistent between different environments or whether they are contingent with respect to their environment (reviewed by Goldberg 1996). If competitive performance involves a trade-off for different resources, the competitive hierarchy will be contingent on the environment and outcomes cannot be predicted in the absence of precise knowledge of environmental conditions, such as resource levels (Tilman 1988, 1990; Silvertown 1989). Asymmetric competition between any two species would not necessarily increase with increasing productivity and, in fact, might even reverse depending on the scale and type of resource limitation. An alternative view is that there are positive correlations in competitive performance for different resources, and thus the degree of asymmetric competition will generally increase with increasing productivity (Grime 1979; Gaudet & Keddy 1988; Keddy 1989; Keddy 1990, 1992). In this case, general predictions can be made in the absence of precise environmental measurements (Gaudet & Keddy 1995). Goldberg (1996) compared 30 studies that tested for consistency vs. contingency of competitive hierarchies among environments, and found that approximately half of them supported each viewpoint.

Resolving different hypotheses about the nature of competitive hierarchies is an important step in developing predictive theories for plant competition. Here, we test whether competitive hierarchies for more than 20 herbaceous shoreline species are consistent in two contrasting environments (high and low nutrients). The phytometer design (Gaudet & Keddy 1988) allows a large number of species to be ranked in terms of relative competitive performance, enabling us to test the generality of the hypothesis for a broad range of species.

Methods

EXPERIMENTAL PROCEDURE

The phytometer, or indicator, method (Gaudet & Keddy 1988, 1995) was used to assess the relative

competitive performance of each of 26 wetland plant species (test species) according to their ability to suppress the growth of a common phytometer (*Penthorum sedoides* L.). This type of comparative, or screening, approach is designed to determine whether individual traits vary consistently across species, and has the additional advantage that a large number of species can be tested concurrently (for examples see Grime *et al.* 1981; Washitani & Masuda 1990; Boutin & Keddy 1993; Reader *et al.* 1993). Phytometer plants were grown from seed in compartmentalized flats containing a sterile organic medium, and placed in a glasshouse that was maintained at approximately 25°C. Ramets of all test species were collected in late April, prior to emergence, from the Ottawa River (Canada) watershed and were taken immediately to the experimental compound for planting. Phytometers were selected for uniformity in size and each individual was planted in the centre of a 1-litre pot filled with sand, surrounded by three individual ramets of one of the 26 test species, planted in a symmetrical pattern. There were 10 replicate pots per species. As we were measuring the competitive effect of the test species on the phytometer, rather than a pair-wise interaction, we used a planting density of 3:1 (test:phytometer). Each species (including *P. sedoides*) was also planted singly under otherwise identical conditions ($n=10$ replicates per species). The pots were placed in an outdoor compound at Carleton University, Ottawa, Ontario, Canada, on 1 May 1988, to coincide with the onset of the natural growing season of these species. Each pot was encircled with mesh screening 15 cm in height (to prevent plants escaping from above-ground competitive interactions within the pot, and to prevent plants from interfering with other pots), and then placed in individual 2-litre plastic tubs. Replicates were arranged in a randomized block design (five blocks) such that each block contained two replicates of each test species plus phytometer, and two replicates of each test species planted singly (control).

Two different nutrient concentrations were established by supplying a modified Hoagland's solution at full-strength to create a 'fertile', high-nutrient, treatment, or at one-tenth of the full strength (infertile, low nutrient). This degree of variation in nutrient supply is known to have significant effects on plant growth (Shiple & Keddy 1988) and therefore created different environments. Moore *et al.* (1989) measured macronutrient levels across a wide range of wetland types in eastern Ontario and western Quebec, ranging from infertile gravel shoreline to fertile sheltered bays: the experimental treatments correspond approximately to the range found in the field. Within each block, one of the replicates of each test species plus phytometer and controls was randomly assigned to each nutrient level, giving five replicates per species/per treatment overall. The

nutrient solution was completely replaced twice a week, when fresh solution was added to the 2-litre tub under each pot. Plants were exposed to normal seasonal precipitation, and during July and August plants were also misted daily to avoid desiccation.

The experiment was conducted over two growing seasons. Above-ground biomass of the phytometer was harvested and dried to constant weight after plant senescence at the end of the first year. The dormant below-ground portions (all but one of the species were perennial) were stored in a cold room at 4°C over winter (November–March) before return to the outdoor compound. Both above- and below-ground biomass of phytometers and test species were harvested, washed (in the case of below-ground biomass), dried and weighed at the end of the second growing season. Biomass was the only measure used because it has been shown to be a good predictor of competitive performance (Gaudet & Keddy 1988, 1995; Grime *et al.* 1997), presumably because of the importance of size-related competitive ability for light (Weiner 1986). Three species (the single annual *Bidens cernua*, and two perennials *Lobelia dortmanna* and *Ranunculus reptans*) did not survive to the end of the second growing season in any replicate and were therefore excluded from analyses of the final harvest.

SPECIES CHARACTERISTICS

Most of the 26 test species, as well as the phytometer, are widespread across eastern North America, where they tend to co-occur on the shores of lakes (Stuckey 1975; Crowder *et al.* 1977; Keddy 1985; Reznicek & Catling 1989; Wilcox & Meeker 1991) and rivers (Dansereau 1959; Auclair *et al.* 1976a; Day *et al.* 1988; Brunton & Di Labio 1989). They were selected because they are typical of seasonally flooded habitats, where there is submergence in May and June, growth in July and August, senescence in September and dormancy after October frosts. Although the species grow freely mixed in a wide array of associations and densities, they are generally sorted to varying degrees along gradients of substrate fertility and exposure to waves, with the smaller evergreen types (e.g. *Lobelia*, *Eriocaulon*, *Ranunculus*) tending to occur largely on open sandy beaches and shores, and the taller canopy-forming types (*Typha*, *Phalaris*, *Penthorum*, *Scirpus*) tending to be restricted to bays. Transplant experiments suggest that, although most species have broad habitat tolerances and physiological performance is best at high fertility, natural distributions are compressed by biological interactions (Wilson & Keddy 1986a, 1988; Twolan-Strutt & Keddy 1996).

Major nutrients, organic matter and silt and clay content are all positively correlated along shoreline gradients (Pearsall 1920; Auclair *et al.* 1976a, b; Day *et al.* 1988; Moore *et al.* 1989), so imposing an

overall fertility gradient seems a reasonable surrogate. Naturally occurring substrates (Wilson & Keddy 1985, 1986a) undoubtedly produce more realistic simulations, but nutrient mixtures (Austin & Austin 1980; Weiher & Keddy 1995) can be reproduced in other experiments. We therefore chose to create an artificial gradient using two different concentrations of a widely recognized nutrient solution.

The species used were selected to represent the full array of plant species in such habitats, constrained only by the difficulties of finding material under a metre of icy water and success in transplanting to pots. Smaller and partially evergreen species included *Juncus pelocarpus* and *Eleocharis acicularis*. Small herbs included *Triadenum fraseri* and *Hypericum ellipticum*; reed-like growth forms included *Eleocharis calva*, *E. palustris* and *Scirpus torreyi*; and tussock growth was represented by *Carex crinita*. One nationally rare species (*Euthamia galetorum*) was obtained in Nova Scotia and flown fresh to Ottawa for transplanting. The largest, canopy-forming, plants were *Typha xglauca* Godr., *Phragmites communis* (Cav.) Trin. and *Phalaris arundinacea* L.

COMPETITIVE PERFORMANCE

Relative competitive performance was calculated as:

$$Cp_i = P_i - P_{2ij}P_i \times 100$$

where Cp_i is the relative competitive performance of the i th species; P_i is the biomass of the phytometer grown alone (control); and P_{2ij} is the weight of the phytometer when grown with the i th species. Because below-ground biomass was not harvested in the first year (to avoid killing all the plants), most analyses of competitive performance were based on relative suppression of above-ground biomass of the phytometer to enable comparison between years.

The relationship between relative competitive performance under low and high nutrient conditions was assessed using correlation analysis (Pearson's r), and linear regression analysis within each year.

Results

EFFECT OF THE EXPERIMENTAL NUTRIENT REGIME ON SPECIES BIOMASS

Before examining the competitive hierarchies, it was important to ascertain that the fertility regimes represented significantly different environmental conditions for the species in this study. When data for all 23 perennial species grown in the presence of the phytometer species after 2 years were pooled, there was indeed a significant effect of the nutrient treatment on above-ground biomass (Fig. 1a): the mean value under high nutrient conditions was 20 times greater than that for low nutrient conditions.

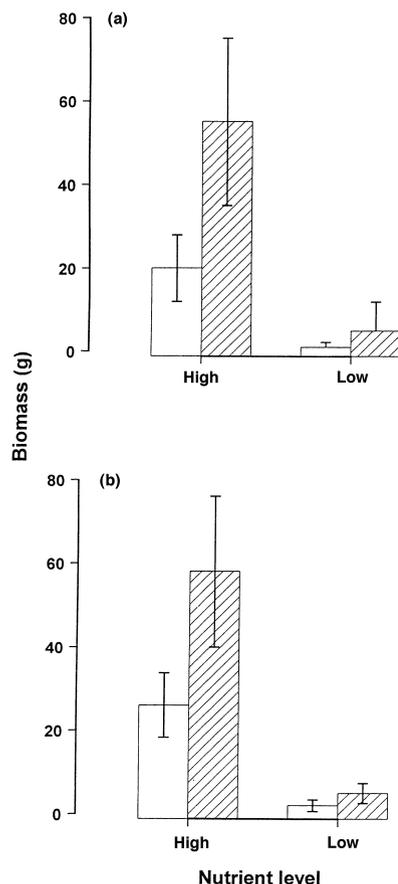


Fig. 1 Mean biomass (g) for 23 shoreline plant species grown under high and low nutrient regimes. See Table 2 for list of species. (a) Above-ground biomass (open bars) and below-ground biomass (dashed bars) of species grown with phytometer; (b) above-ground biomass (open bars) and below-ground biomass (dashed bars) of species grown singly (control). Error bars represent 95% confidence limits. When data for all 23 species were pooled, biomass under high and low nutrient conditions was significantly different for each of the above- conditions as follows: (a) above-ground, $t = 5.33$, $P < 0.001$; below-ground, $t = 3.71$, $P < 0.001$; (b) above-ground, $t = 6.24$, $P < 0.001$; below-ground, $t = 4.42$, $P < 0.001$.

The different nutrient regimes also had a significant effect on test species' below-ground biomass (Fig. 1b). These results were not a consequence of altered competitive interactions under high and low nutrient conditions, as similar effects were noted in the same species grown singly (Tables 1 and 2). When data for all 23 species were pooled, there was also a significant increase in the ratio of below- to above-ground biomass allocation under low nutrient conditions (Fig. 2).

INTENSITY OF COMPETITION

When the biomass of phytometers grown singly ($n = 10$) was compared with the biomass of phyt-

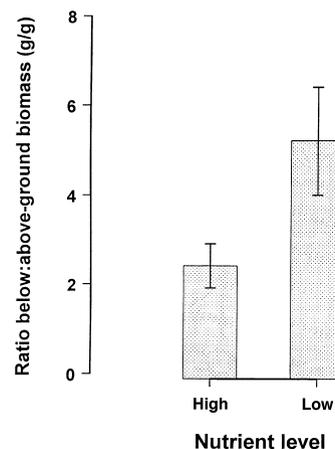


Fig. 2 Mean ratio of below-ground to above-ground biomass (g/g) for 23 shoreline plant species grown under high and low nutrient regimes. See Table 2 for list of species. Error bars represent 95% confidence limits. When data for all 23 species were pooled, the ratio of below- to above-ground biomass significantly different between high and low nutrient conditions (Mann-Whitney $z = 4.02$; $P < 0.0001$).

ometers grown with neighbours under high nutrient ($n = 114$) and low nutrient ($n = 107$) conditions, a Kruskal-Wallis one-way analysis of variance by ranks showed that competition had a significant effect on phytometer biomass under both high ($k = 2$; $H = 19.16$; $P < 0.0001$) and low nutrient conditions ($k = 2$; $H = 8.76$; $P < 0.0005$). Although there was a significant competitive effect under each nutrient regime, the intensity of the effect varied between the conditions. Under high nutrient conditions, the phytometer was suppressed by an average of 58%, compared with 34% under low nutrient conditions, indicating that competition was less intense under low nutrient conditions (Fig. 3); a Kruskal-Wallis analysis of variance by ranks showed that this treatment effect was significant.

COMPETITIVE HIERARCHIES

Competitive hierarchies, using above-ground biomass to allow comparison across years, at the end of the first and second growing seasons are shown in Tables 1 and 2. In each case, a one-way analysis of variance showed that there was a significant species effect on percentage reduction of the phytometer biomass (year 1 low nutrient: $k = 26$; $H = 88.99$; $P < 0.0001$; year 1 high nutrient: $k = 26$; $H = 119.23$; $P < 0.0001$; year 2 low nutrient: $k = 23$; $H = 97.44$; $P < 0.0001$; year 2 high nutrient: $k = 23$; $H = 104.13$; $P < 0.0001$). It was therefore reasonable to rank species in terms of relative competitive performance for each year and treatment level.

Table 1 Relative competitive performance for 26 shoreline plant species (in rank order) under high and low nutrient conditions after one growing season. Relative competitive performance was estimated as the percentage reduction in above-ground biomass of a common phytometer *Penthorum sedoides* ($n = 5$ replicates per species)

High nutrient		Low nutrient	
Species	% Reduction in phytometer biomass (SD)	Species	% Reduction in phytometer biomass (SD)
<i>Lythrum salicaria</i>	96 (1.40)	<i>Sparganium eurycarpum</i>	57 (5.16)
<i>Bidens cernua</i>	94 (2.31)	<i>Typha xglauca</i>	56 (5.36)
<i>Sparganium eurycarpum</i>	94 (2.68)	<i>Spartina pectinata</i>	55 (11.82)
<i>Typha xglauca</i>	93 (4.26)	<i>Bidens cernua</i>	52 (13.48)
<i>Mentha arvensis</i>	88 (8.15)	<i>Eleocharis calva</i>	52 (15.82)
<i>Scirpus fluviatilis</i>	86 (6.63)	<i>Eleocharis acicularis</i>	48 (13.86)
<i>Rumex verticillatus</i>	86 (5.16)	<i>Eleocharis palustris</i>	46 (14.49)
<i>Phragmites australis</i>	82 (6.40)	<i>Scirpus fluviatilis</i>	45 (10.38)
<i>Phalaris arundinacea</i>	78 (7.64)	<i>Acorus calamus</i>	44 (8.84)
<i>Spartina pectinata</i>	77 (4.44)	<i>Phragmites australis</i>	40 (13.16)
<i>Acorus calamus</i>	73 (2.31)	<i>Rumex verticillatus</i>	37 (18.24)
<i>Eleocharis palustris</i>	50 (8.78)	<i>Juncus filiformis</i>	35 (7.76)
<i>Euthamia galetorum</i>	48 (4.63)	<i>Carex crinita</i>	34 (8.00)
<i>Eleocharis calva</i>	45 (18.28)	<i>Phalaris arundinacea</i>	31 (20.76)
<i>Carex crinita</i>	43 (7.72)	<i>Mentha arvensis</i>	29 (11.63)
<i>Dulichium arundinaceum</i>	30 (13.44)	<i>Lythrum salicaria</i>	29 (12.90)
<i>Eleocharis acicularis</i>	22 (8.84)	<i>Ranunculus reptans</i>	24 (12.75)
<i>Triadenum fraseri</i>	19 (4.70)	<i>Triadenum fraseri</i>	19 (10.66)
<i>Lysimachia terrestris</i>	19 (5.48)	<i>Viola lanceolata</i>	19 (11.37)
<i>Ranunculus reptans</i>	19 (3.78)	<i>Hypericum ellipticum</i>	15 (16.30)
<i>Juncus pelocarpus</i>	15 (11.70)	<i>Lysimachia terrestris</i>	14 (17.13)
<i>Juncus filiformis</i>	11 (11.24)	<i>Scirpus torreyi</i>	1 (16.10)
<i>Viola lanceolata</i>	6 (16.42)	<i>Juncus pelocarpus</i>	-1 (10.64)
<i>Hypericum ellipticum</i>	4 (10.40)	<i>Dulichium arundinaceum</i>	-1 (15.23)
<i>Lobelia dortmanna</i>	1 (5.70)	<i>Lobelia dortmanna</i>	-5 (15.30)
<i>Scirpus torreyi</i>	-4 (2.56)	<i>Euthamia galetorum</i>	-5 (9.82)

Figure 4 shows that competitive performance under high and low nutrient conditions was significantly correlated in both year 1 ($r_s = 0.65$; $P < 0.005$; $n = 26$) and year 2 ($r_s = 0.76$; $P < 0.0005$; $n =$

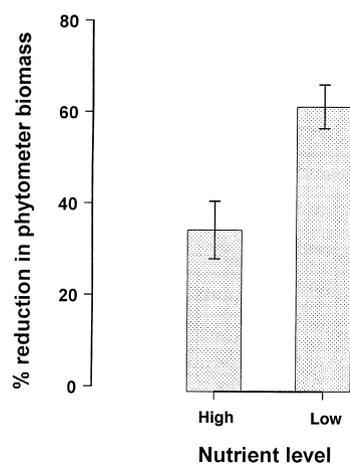


Fig. 3 Mean percentage reduction in phytometer biomass when data for all 23 species are pooled under high and low nutrient conditions. See Table 2 for list of species. Error bars represent 95% confidence limits. There is a significant effect of nutrient treatment on percentage reduction in phytometer biomass (Kruskal–Wallis analysis of variance by ranks: $n = 114\ 107$; $k = 2$; $H = 20.78$; $P < 0.0001$).

23). When a single outlier (*Rumex verticillatus*) was removed in the analysis for the second year, the r_s increased to 0.84 ($P < 0.001$). This genus is known to be a concentrator of phosphorus and also showed an anomalous result in work done by McJanet *et al.* (1995). A *Rumex* sp. was also found to be a significant outlier to the general relationship in a study of competition in mown fields (Fowler 1982).

The relative competitive performance of species was correlated between years under high nutrient conditions (Fig. 5a), suggesting that the hierarchy formed under high nutrient conditions is relatively invariant over time. In contrast, the competitive performance of species under low nutrient conditions showed no significant relationship between years (Fig. 5b). It may be that, under low nutrient conditions, a longer period of time is required to establish a hierarchy, and this may explain why the correlation between competitive performance under high and low nutrient conditions shown in Fig. 4 was stronger in the second year.

ABOVE- VS. BELOW-GROUND HIERARCHIES

The hierarchies and relationships described above were based on above-ground biomass of the phyt-

Table 2 Relative competitive performance for 23 shoreline plant species under high and low nutrient conditions after two growing seasons. Relative competitive performance was estimated as the percentage reduction in both above- and below-ground biomass of a common phytometer *Penthorum sedoides*. Numbers of species vary between years due to overwinter mortality (*R. reptans*, *L. dortmanna*) or because the species was an annual (*B. cernua*). ($n = 5$ except for species marked *, where $n = 4$)

High nutrient			Low nutrient		
Species	Reduction in phytometer biomass (%)		Species	Reduction in phytometer biomass (%)	
	Above	Below		Above	Below
<i>Typha xglauca</i>	99 (0.80)	97 (1.27)	<i>Lythrum salicaria</i> *	95 (4.68)	91 (5.44)
<i>Spartina pectinata</i>	97 (1.16)	97 (2.23)	<i>Phalaris arundinacea</i>	84 (4.70)	80 (5.23)
<i>Phalaris arundinacea</i>	94 (3.06)	95 (2.98)	<i>Spartina pectinata</i>	79 (16.90)	80 (16.84)
<i>Phragmites australis</i> *	92 (7.63)	89 (7.78)	<i>Typha xglauca</i>	78 (5.47)	70 (6.81)
<i>Scirpus fluviatilis</i>	92 (2.48)	93 (2.69)	<i>Euthamia galetorum</i> *	69 (5.50)	65 (6.12)
<i>Sparganium eurycarpum</i>	91 (2.31)	85 (4.24)	<i>Mentha arvensis</i>	69 (12.56)	70 (10.49)
<i>Mentha arvensis</i>	90 (5.77)	91 (4.67)	<i>Acorus calamus</i>	63 (5.40)	75 (7.80)
<i>Lythrum salicaria</i>	89 (4.75)	79 (5.70)	<i>Phragmites australis</i>	58 (7.39)	55 (8.19)
<i>Euthamia galetorum</i>	88 (4.87)	90 (5.69)	<i>Juncus filiformis</i>	56 (8.24)	60 (7.54)
<i>Rumex verticillatus</i>	83 (6.46)	80 (7.43)	<i>Eleocharis palustris</i> *	39 (10.20)	51 (12.72)
<i>Acorus calamus</i>	74 (12.22)	91 (15.54)	<i>Sparganium eurycarpum</i>	39 (13.50)	40 (10.11)
<i>Eleocharis calva</i>	62 (14.66)	58 (12.38)	<i>Eleocharis calva</i> *	35 (10.24)	39 (11.88)
<i>Eleocharis palustris</i>	61 (17.76)	59 (14.56)	<i>Lysimachia terrestris</i>	32 (16.00)	40 (15.65)
<i>Lysimachia terrestris</i>	53 (11.32)	50 (12.19)	<i>Dulichium arundinaceum</i>	24 (10.93)	25 (9.02)
<i>Carex crinita</i>	46 (12.64)	32 (9.68)	<i>Scirpus fluviatilis</i>	23 (6.48)	31 (8.42)
<i>Juncus filiformis</i>	34 (5.87)	36 (6.32)	<i>Triadenum fraseri</i>	17 (15.05)	20 (14.89)
<i>Dulichium arundinaceum</i>	25 (5.52)	58 (13.54)	<i>Carex crinita</i>	7 (13.00)	15 (11.69)
<i>Hypericum ellipticum</i>	22 (12.60)	20 (9.38)	<i>Viola lanceolata</i> *	5 (14.53)	6 (15.92)
<i>Eleocharis acicularis</i>	17 (10.99)	15 (8.72)	<i>Juncus pelocarpus</i>	-15 (12.84)	10 (10.90)
<i>Juncus pelocarpus</i>	10 (8.07)	9 (5.73)	<i>Hypericum ellipticum</i>	-16 (9.17)	-2 (8.22)
<i>Triadenum fraseri</i>	8 (2.96)	10 (3.15)	<i>Eleocharis acicularis</i> *	-18 (9.20)	3 (5.38)
<i>Viola lanceolata</i>	6 (4.40)	5 (5.21)	<i>Rumex verticillatus</i>	-18 (17.81)	-10 (15.32)
<i>Scirpus torreyi</i>	1 (21.02)	4 (16.99)	<i>Scirpus torreyi</i> *	-19 (16.79)	-4 (20.30)

ometer to enable comparison between years. It is possible that the below-ground competition is important, especially under low nutrient conditions. However, phytometer biomass (a direct measure of competitive performance) measured above- and below-ground for each test species was highly correlated under both high ($r_s = 0.94$; $P < 0.00001$; $n = 23$) and low nutrient conditions ($r_s = 0.71$; $P < 0.001$; $n = 23$).

It is also possible that test species' traits contribute differently to competitive performance above- and below-ground (Gaudet & Keddy 1988). Although the experiment was not designed to test this directly, biomass measures were made on the test species at the time of harvest. Table 3 summarizes the relationship between test species' biomass and competitive effect above- and below-ground. Under high nutrient conditions, the above-ground biomass of the test species was highly negatively correlated with phytometer biomass both above- and below-ground, as was the below-ground biomass. The correlations under low nutrient conditions were certainly not as high, especially involving the below-ground component, but most were significant. Perhaps below-ground biomass of the phyt-

ometer biomass varied independently of competitive performance under low nutrient conditions, a possibility that is consistent with other work (Wilson 1988) showing that species generally allocate a higher proportion of biomass below-ground under low nutrient conditions.

Discussion

COMPETITIVE HIERARCHIES

Although shifts in the ranking of species were apparent between high and low nutrient conditions, there were predictable patterns at the multispecies scale, and statistical comparison between treatments indicated that there was a significant positive relationship between species' competitive performance at high and low fertility. In general, irrespective of nutrient level, large leafy species typical of fertile habitats (e.g. *Lythrum salicaria*, *Sparganium eurycarpum*, *Typha xglauca*) emerged near the top of the hierarchy, as would be predicted from other studies (Day *et al.* 1988; Weiher & Keddy 1995; Keddy *et al.* 1997). Small rosette species (*Lobelia dortmanna*, *Viola lanceolata*) and partially evergreen species

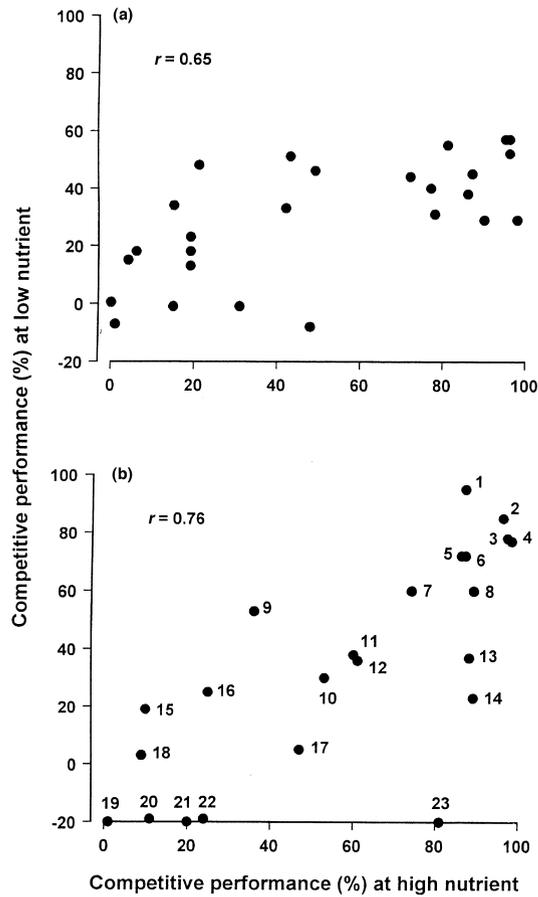


Fig. 4 Relationship between competitive performance under low nutrient conditions and competitive performance under high nutrient conditions; (a) year 1 results; (b) year 2 results. Species names are indicated only for year 2 results as follows: 1, *Lythrum salicaria*; 2, *Phalaris arundinacea*; 3, *Phragmites communis*; 4, *Typha xglauca*; 5, *Euthamia galetorum*; 6, *Mentha arvensis*; 7, *Acorus calamus*; 8, *Spartina pectinata*; 9, *Juncus filiformis*; 10, *Lysimachia terrestris*; 11, *Eleocharis palustris*; 12, *Eleocharis calva*; 13, *Sparganium eurycarpum*; 14, *Scirpus fluviatilis*; 15, *Triadenum Fraseri*; 16, *Dulichium arundinaceum*; 17, *Carex crinita*; 18, *Viola lanceolata*; 19, *Scirpus torreyi*; 20, *Juncus pelocarpus*; 21, *Eleocharis acicularis*; 22, *Hypericum ellipticum*; 23, *Rumex verticillatus*.

typical of infertile habitats (*Juncus pelocarpus*, *Eleocharis acicularis*, *Ranunculus reptans*) were near the bottom of the hierarchy, which is consistent with other studies (Goldsmith 1978; Wilson & Keddy 1986b; Givnish 1988; Grime *et al.* 1997). Therefore, the main axis appears to represent growth form, which in turn varies with habitat.

While our study was not set up to explore mechanisms underlying competitive performance, these size-related patterns do suggest such an interpretation. Large plants have larger surface areas for extracting resources from the environment, and therefore also have a greater ability to create nutrient-depletion zones irrespective of resource levels (Campbell *et al.* 1991). In the case of light, large

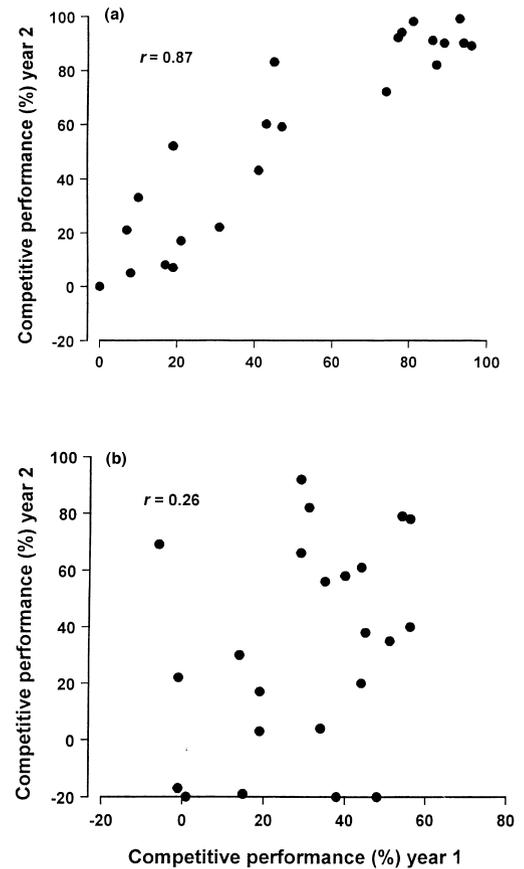


Fig. 5 Relationship between mean competitive performance of species ($n = 23$ species) over two growing seasons under (a) high nutrient conditions and (b) low nutrient conditions. See Table 2 for species list.

plants, being generally taller, can intercept light, thereby denying it to smaller neighbours, leading to asymmetric interactions (Weiner 1985, 1986; Keddy & Shipley 1989; Keddy 1989). Superimposed differences in nutrient uptake rates per unit surface area, or differences in efficiency of use or conservation, may contribute to the residual variation.

It is noteworthy that the most obvious shifts in competitive performance occurred under low nutrient conditions between years 1 and 2. For example, *Eleocharis acicularis*, a small lanceolate-leaved plant, induced a 48% reduction in the phytometer in the first year at low fertility, but promoted growth (competitive performance = -18%) in the second year. On the other hand, the relative performance in the presence of *Euthamia galetorum*, a large leafy plant that can reach a height of up to 1 m, was -5% in the first year, compared with 69% in year 2. One possible interpretation is that position in the competitive hierarchy is more variable under low fertility conditions. This might be expected if competitive hierarchies under fertile conditions result from strong asymmetric competition for light (Weiner

Table 3 Correlation (r) of above- and below-ground biomass of phytometer *Penthorum sedoides* with above- and below-ground biomass and root/shoot ratios of test species ($n = 23$) under high and low nutrient conditions over two growing seasons. Phytometer biomass is a direct measure of the competitive performance of the test species and calculated as percentage reduction in phytometer biomass to which it is inversely related; NS = not significant at the 0.05 level

			Phytometer biomass (g)		
			Above	Below	Total
Test species biomass (g)	High nutrient	Total	High nutrient		
			–0.85	–0.78	–0.83
			$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
		Above	–0.93	–0.85	–0.91
			$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
			–0.78	–0.74	–0.77
	Low nutrient	Total	Low nutrient		
			–0.49	–0.41	–0.45
			$P = 0.02$	$P = 0.05$	$P = 0.03$
		Above	–0.57	–0.43	–0.50
			$P = 0.004$	$P = 0.04$	$P = 0.01$
			–0.49	–0.41	–0.44
Below : above	Below : above	–0.43	–0.51	–0.47	
		$P = 0.04$	$P = 0.01$	$P = 0.02$	
		NS	NS	NS	
	Below : above	–0.30	–0.40	–0.34	
		$P = 0.02$	NS	$P = 0.03$	
		NS	NS	NS	

1986; Keddy 1989), leading to a clear winner and loser. In contrast, under infertile conditions, root competition may predominate, which may be more symmetric (Weiner 1986) with no pronounced dominance/suppression. Shifts in competitive rankings may result when there is no asymmetric advantage that is maintained and reinforced over time.

At low productivity, competitive hierarchies may also be influenced by mycorrhizae. When mineral nutrient concentration is high, the rate of mycorrhizal infection is relatively low (Smith & Read 1997), whereas at low productivity mycorrhizae play a much more important role in the acquisition of mineral nutrients. Grime *et al.* (1987) grew seedlings of 20 grassland plants in a mixture with larger *Festuca ovina* plants, both with and without mycorrhizae. Although the mycorrhizae had little impact on the performance of *Festuca ovina* seedlings that were competing with larger plants of the same species, the balance between *Festuca ovina* and seedlings of other species was affected. Thus, mycorrhizae may play a role in interspecific competition (Fitter 1977; Allen & Allen 1990; Watkinson & Freckleton 1997).

The reduced intensity of competition under low nutrient conditions may also be important in accounting for shifts in ranking. As competition intensity decreases, other factors may become increasingly important as determinants of plant biomass. However, an alternative explanation is that under conditions of low fertility, plants may simply take longer to establish an hierarchy, and this is supported by the increasing correlation between

ranking at high and low fertility over the course of the experiment.

Wilson (1988) suggested that root and shoot competition vary independently, but our results do not support this view for shoreline plant species. However, root and shoot competition were not studied independently, and it may be that if species had been prevented from competing above-ground, below-ground competition alone would have resulted in a different hierarchy. The results, however, do support the work by Twolan-Strutt & Keddy (1996), which showed that below-ground competition intensity did not vary between different shoreline habitats.

CONTINGENCY AND SCALE

The contrasting views about competitive hierarchies and contingency appear to represent results from two different scales rather than opposing inconsistent views, and it is therefore important to distinguish between coarse- and fine-scale relationships. The current study was designed to explore a general coarse-scale pattern across a large number of species in two very different habitats. In contrast, fine-scale work on small numbers of species, particularly ones with similar ecological requirements, may emphasize contingency and possibly miss general predictive relationships. In fact, one could argue that the past emphasis upon contingency has arisen because the majority of experiments used a few pairs of species in varied environments and were by their very design capable of detecting only contingency.

However, although larger scale comparative work may provide general predictive relationships, it might overlook the details of species' interactions that contribute to the understanding of fine-scale pattern and mechanism in the field. The fine-scale pattern seen in small plots may depend on competitive interactions between pairs of species that are similar in competitive performance, as it has been suggested that such equivalence is likely to foster coexistence of species (Aarssen 1983, 1985). It is at this scale, where competitive interactions may be increasingly symmetrical (*sensu* Wilson 1988; Keddy 1989), that contingency may be most pronounced and minor fluctuations in the environment may have a major influence on dominance. For example, Grace & Wetzel (1981) found that water depth played a critical role in determining competitive dominance between two closely associated species of *Typha*.

Our results suggest that, at the broad community scale, the outcome of competitive interactions may be relatively predictable and independent of the environment. Such studies therefore provide a useful tool for exploring and understanding community pattern, but cannot address questions related to the outcome of competitive interactions between similar species or within fine-scale pattern. Further empirical work is needed to sort out the factors that may be operating at different scales of organization.

INTENSITY OF COMPETITION

Our results indicate that, while competitive hierarchies do exist at low nutrient levels, the intensity of competition is reduced by approximately 25% relative to fertile conditions. Similar results have been obtained for shoreline plant communities by Wilson & Keddy (1986a) in a field study of diffuse competition, as well as for grassland species (Campbell & Grime 1992; Peltzer *et al.* 1998) and moorland species (Hartley & Amos 1999). The hypothesis (Grime 1979; Huston 1979) that factors other than competition may be increasingly important in structuring natural communities under infertile conditions therefore receives general support. Although this experiment was not designed to test directly for the importance or intensity of competition (*sensu* Welden & Slauson 1986), its results indicate that competition intensity, measured as the relative decrease in biomass of the phytometer across all species, was lower under stressful infertile conditions, as suggested by Grime (1979, 1988). This may in part explain why species of high relative competitive performance are not equally dominant throughout the gradient. However, the fact that competitive performance, although reduced, is still significant under low nutrient conditions means that declining

soil fertility altering the nature of competition from above-ground to below-ground resources (Newman 1973; Tilman 1988, 1990; Wilson 1988) is an alternative explanation. However, the supposition that competition will become more intense or important as resources are increasingly limited (Fowler 1986) is not supported, at least with respect to nutrient levels.

The results were based on a comparison of only two nutrient levels, and it is not known how results would have varied with other nutrient regimes. Nor do we know how the results would have changed over a longer period of time [Tilman (1988), and Berendse & Elberse (1990) show that time span may be an important consideration when evaluating competitive performance].

More studies at the community scale are needed to assess how other environmental variables or different nutrient levels will influence plant hierarchies. There are few studies using large numbers of species in contrasting environments, so generalization about the consistency of competitive hierarchies is not yet possible. However, the phytometer approach makes such studies more feasible than past pair-wise designs, which increased the size of experiments by the square of the number of species examined. It may be that different patterns will emerge, particularly in traits associated with competitive performance, if different floras are examined. If wetlands are generally light limited, it may be that hierarchies are produced by different competitive abilities for light based on above-ground traits, whereas in other habitats, such as prairies and deserts, hierarchies could be associated with below-ground traits.

The results of this experiment have two important implications for community ecology. First, they illustrate that scale must be considered. General questions about the community level of organization are probably best answered by experiments examining simultaneously large numbers of species of contrasting ecology (Keddy 1992). Secondly, our results show that position in competitive hierarchies is relatively consistent. This has two further implications for the study of plant competition: first, that it is reasonable to test for specific traits that can predict competitive performance, and secondly, that competitive hierarchies can provide a general framework for exploring the structure of communities.

Acknowledgements

We thank two anonymous referees and L. Haddon for their helpful comments on earlier drafts of the manuscript. Financial support was provided by a Natural Science and Engineering Research Council grant to P. Keddy.

References

- Aarssen, L.W. (1983) Ecological combining ability and competitive combining ability in plants: towards a general evolutionary theory of coexistence in systems of competition. *American Naturalist*, **122**, 707–731.
- Aarssen, L.W. (1985) Interpretation of the evolutionary consequences of competition in plants: an experimental approach. *Oikos*, **45**, 99–100.
- Allen, E.B. & Allen, M.F. (1990) The mediation of competition by mycorrhizae in successional and patchy environments. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 367–389. Academic Press, San Diego.
- Auclair, A.N.D., Bouchard, A. & Pajaczkowski, J. (1976a) Plant standing crop and productivity relations in a *Scirpus-Equisetum* wetland. *Ecology*, **57**, 941–952.
- Auclair, A.N.D., Bouchard, A. & Pajaczkowski, J. (1976b) Productivity relations in a *Carex*-dominated ecosystem. *Oecologia*, **26**, 9–31.
- Austin, M.P. & Austin, B.O. (1980) Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology*, **68**, 891–918.
- Berendse, F. & Elberse, W.T. (1990) Competition, succession, and nutrient availability. *Perspectives on Plant Competition* (eds J. Grace & D. Tilman), pp. 93–116. Academic Press Inc, San Diego, CA.
- Boutin, C. & Keddy, P.A. (1993) A functional classification of wetland plants. *Journal of Vegetation Science*, **4**, 591–600.
- Brunton, D.F. & Di Labio, B.M. (1989) Diversity and ecological characteristics of emergent beach flora along the Ottawa river in the Ottawa-Hull region, Quebec and Ontario. *Naturaliste Canadien*, **116**, 179–191.
- Campbell, B.D. & Grime, J.P. (1992) An experimental test of plant strategy theory. *Ecology*, **73**, 15–29.
- Campbell, B.D., Grime, J.P., Mackey, J.M.L. & Jalili, A. (1991) The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Functional Ecology*, **5**, 241–253.
- Crowder, J., Bristow, M. & King, M.R. (1977) The aquatic macrophytes of some lakes in southeastern Ontario. *Naturaliste Canadien*, **104**, 457–464.
- Dansereau, P. (1959) Vascular aquatic plant communities of southern Quebec. A preliminary analysis. *Transactions of the Northeast Wildlife Conference*, **10**, 27–54.
- Day, R.T., Keddy, P.A., McNeill, J. & Carleton, T. (1988) Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology*, **69**, 1044–1054.
- Fitter, A.H. (1977) Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytologist*, **79**, 119–125.
- Fowler, N. (1982) Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. *Journal of Ecology*, **70**, 77–92.
- Fowler, N. (1986) The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**, 89–105.
- Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.
- Gaudet, C.L. & Keddy, P.A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology*, **76**, 280–291.
- Givnish, T.J. (1988) Ecology and evolution of carnivorous plants. *Plant-Animal Interactions* (ed. W.G. Abrahamson), pp. 243–290. McGraw-Hill, New York, NY.
- Goldberg, D.E. (1996) Competitive ability: definitions, contingency and correlated traits. *Philosophical Transactions of the Royal Society of London B*, **351**, 1377–1385.
- Goldsmith, F.B. (1978) Interaction (competition) studies as a step towards the synthesis of seacliff vegetation. *Journal of Ecology*, **66**, 921–931.
- Grace, J.B. & Wetzel, R.G. (1981) Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist*, **118**, 463–474.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley, Chichester, UK.
- Grime, J.P. (1988) The C-S-R model of primary strategies: origins, implications and tests. *Plant Evolutionary Biology* (eds L.D. Gottlieb & S.K. Jain), pp. 371–393. Chapman & Hall, London, UK.
- Grime, J.P., Mowforth, M.A.G., Neal, A.M. & Shaw, S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**, 1017–1059.
- Grime, J.P., Mackey, J.M.L., Hillier, S.H. & Read, D.J. (1987) Floristic diversity in a model system using experimental microcosms. *Nature*, **328**, 420–422.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodgkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. & Whitehouse, J. (1997) Integrated screening validates a primary axis of specialisation in plants. *Oikos*, **97**, 259–281.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Hartley, S.E. & Amos, S. (1999) Competitive interactions between *Nardus stricta* L. and *Calluna vulgaris* (L.) Hull: the effect of fertilizer and defoliation on above- and below-ground performance. *Journal of Ecology*, **87**, 330–340.
- Huston, M. (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.
- Johansson, M.E. & Keddy, P.A. (1991) Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. *Oikos*, **60**, 27–34.
- Keddy, P.A. (1985) Lakeshore plants in the Tusket River Valley, Nova Scotia: the distribution and status of some rare species including *Coreopsis rosea* and *Sabatia kennedyana*. *Rhodora*, **87**, 309320.
- Keddy, P.A. (1989) *Competition*. Chapman & Hall, London, UK.
- Keddy, P.A. (1990) Competitive hierarchies and centrifugal organization in plant communities. *Perspectives in Plant Competition* (eds J.B. Grace & D. Tilman), pp. 265–290. Academic Press, New York, NY.
- Keddy, P.A. (1992) A pragmatic approach to functional ecology. *Functional Ecology*, **6**, 621–626.
- Keddy, P.A. & Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos*, **54**, 234–241.
- Keddy, P., Twolan-Strutt, L. & Shipley, B. (1997) Experimental evidence that interspecific competitive asymmetry increases with soil productivity. *Oikos*, **80**, 253–256.
- McJannet, C.L., Keddy, P.A. & Pick, F.R. (1995) Nitrogen and phosphorus tissue concentrations in 41

- wetland plants: a comparison across habitats and functional groups. *Functional Ecology*, **9**, 231–238.
- Mitchley, J. & Grubb, P.J. (1986) Control of relative abundance of perennials in chalk grassland in southern England. *Journal of Ecology*, **74**, 1139–1166.
- Moore, D.R.J., Keddy, P.A., Gaudet, C.L. & Wisheu, I.C. (1989) Conservation of wetlands: do infertile wetlands deserve a higher priority? *Biological Conservation*, **47**, 203–217.
- Newman, E.I. (1973) Competition and diversity in herbaceous vegetation. *Nature*, **244**, 310.
- Pearsall, W.H. (1920) The aquatic vegetation of the English lakes. *Journal of Ecology*, **8**, 163–201.
- Peltzer, D.A., Wilson, S.D. & Gerry, A.K. (1998) Competition intensity along a productivity gradient in a low-diversity grassland. *American Naturalist*, **151**, 465–476.
- Reader, R.J., Jalili, A., Grime, J.P., Spencer, R. & Matthews, N. (1993) A comparative study of plasticity in seedling rooting depth in drying soil. *Journal of Ecology*, **81**, 543–550.
- Reznicek, A.A. & Catling, P.M. (1989) Flora of Long Point. *Michigan Botanist*, **28**, 99–175.
- Shiple, B. (1993) A null model of competitive hierarchies in competition matrices. *Ecology*, **74**, 1693–1699.
- Shiple, B. & Keddy, P.A. (1988) The relationship between relative growth rate and sensitivity to nutrient stress in 28 species of emergent macrophytes. *Journal of Ecology*, **76**, 1101–1110.
- Shiple, B. & Keddy, P.A. (1994) Evaluating the evidence for competitive hierarchies in plant communities. *Oikos*, **69**, 340–345.
- Smith, S.E. & Read, D.J. (1997) *Mycorrhizal Symbiosis*, 2nd edn. Academic Press, San Diego, CA.
- Silvertown, J. (1989) Plant competition. *Nature*, **337**, 122–123.
- Silvertown, J., Dodd, M.E., McConway, K., Potts, J. & Crawley, M. (1994) Rainfall, biomass variation and community composition in the Park Grass experiment. *Ecology*, **75**, 2430–2437.
- Stuckey, R.L. (1975) A floristic analysis of the vascular plants of a marsh at Perry's Victory Monument, Lake Erie. *Michigan Botanist*, **14**, 144–166.
- Tilman, D. (1988) *Plant Strategies and the Structure and Dynamics of Plant Communities*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1990) Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. *Perspectives on Plant Competition* (eds J. Grace & D. Tilman), pp. 117–141. Academic Press, New York, NY.
- Twolan-Strutt, L. & Keddy, P.A. (1996) Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology*, **77**, 259–270.
- Washitani, I. & Masuda, M. (1990) A comparative study of the germination characteristics of seeds from a moist tall grassland community. *Functional Ecology*, **4**, 543–557.
- Watkinson, A.R. & Freckleton, R.P. (1997) Quantifying the impact of arbuscular mycorrhiza on plant competition. *Journal of Ecology*, **85**, 541–546.
- Weihner, E. & Keddy, P.A. (1995) The assembly of experimental wetland plant communities. *Oikos*, **73**, 323–335.
- Weiner, J. (1985) Size hierarchies in experimental populations of annual plants. *Ecology*, **66**, 743–752.
- Weiner, J. (1986) How competition for light and nutrients affects size variability in *Ipomea tricolor* populations. *Ecology*, **67**, 1425–1427.
- Weldon, C.W. & Slauson, W.L. (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *American Naturalist*, **61**, 23–44.
- Wilcox, D.A. & Meeker, J.E. (1991) Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. *Canadian Journal of Botany*, **69**, 1542–1551.
- Williams, E.J. (1962) The analysis of competition experiments. *Australian Journal of Biological Sciences*, **15**, 509–525.
- Wilson, J.B. (1988) Shoot competition and root competition. *Journal of Applied Ecology*, **25**, 279–296.
- Wilson, S.D. & Keddy, P.A. (1985) Plant zonation on a shoreline gradient: physiological response curves of component species. *Journal of Ecology*, **73**, 851–860.
- Wilson, S.D. & Keddy, P.A. (1986a) Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, **67**, 1236–1242.
- Wilson, S.D. & Keddy, P.A. (1986b) Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist*, **127**, 862–869.
- Wilson, S.D. & Keddy, P.A. (1988) Species richness, survivorship, and biomass accumulation along an environmental gradient. *Oikos*, **53**, 375–380.

Received 20 April 1999

revision accepted 22 October 1999