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Responses of 21 wetland species to shortages of light, nitrogen and phosphorus

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Summary

1 Mineral nutrients and light, among many other factors, can limit plant growth. Tilman's resource ratio hypothesis predicts that there is a trade-off between the abilities of plant species to tolerate low supply rates of nutrients and of light due to a trade-off in allocation between shoots and roots. The hypothesis also predicts that species able to tolerate a lower supply rate of a limiting resource are competitively superior. To test these predictions, we examined how the abilities of wetland plants to tolerate low supply rates of three different resources are related to each other and to their competitive abilities.

2 We determined the effects of low nitrogen, low phosphorus and low light on the growth of 21 species of wetland plants in pots grown outdoors over one growing season. These data were used to determine the relative performance, measured as average biomass under low resource supply divided by average biomass under high resource supply for each of the three resources.

3 Low levels of all three resources caused a significant reduction in performance, with low nitrogen having the greatest effect. The biomass of the 21 species under low resource supply was positively correlated with their biomass under high resource supply. By contrast, relative performance under low resource supply was uncorrelated (low light, low phosphorus) or negatively correlated (low nitrogen) with the species' biomass under high resource supply. There were no correlations between relative performance under low levels of different resources, i.e. no evidence for a trade-off. Therefore, our results do not support the first of the predictions derived from Tilman's hypothesis.

4 Relative performance under low resource supply was compared with independent, published measures of competitive effect and competitive response. Performance under low nitrogen was negatively correlated with competitive ability in terms of both competitive effect and competitive response. Neither performance under low light nor performance under low phosphorus were correlated with either measure of competitive ability. Thus, the second prediction derived from Tilman's hypothesis was not supported either.

Keywords: competitive response, limiting factor, resource ratio hypothesis, stress tolerance

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Introduction

The growth and development of plants is almost always limited by at least one resource, whether it be a mineral nutrient, light, or water. Plants must be able to tolerate varying degrees of resource shortage in order to survive, grow, and reproduce, since they rarely grow at their optimal resource supply. Resources may be limited either because of inherent shortages within the physical environment (Chapin 1980; Levitt 1980; Marschner 1995) or because of depletion by neighbouring plants (Harper 1963, Grime 1979; Tilman 1982, 1988).

Often, one resource is much more limited than the others. It is known that plant species differ in their abilities to tolerate low levels of different resources, but there still is disagreement on how these abilities are related with each other. For example, is a plant species that performs well under low nutrient supply also particularly shade-tolerant or, on the contrary, does it have rather high requirements for light? A related debate centers around whether or not there is a trade-off between the abilities of species to compete for limiting resources above ground (light) and below ground (mineral nutrients). According to Tilman's resource ratio hypothesis (1982, 1988) the two questions are equivalent because a species able to tolerate the lowest level of a resource R will competitively exclude other species when resource R is limiting, and therefore have a high ability to compete for this resource.

A number of researchers have suggested that there is an inverse relationship between above- and below-ground competitive abilities (Newman 1973; Grubb 1985; Tilman 1987, 1988; Huston & Smith 1987). It is proposed that this inverse relationship arises because allocation of a resource to one structure precludes allocation to another, resulting in morphological trade-offs (Iwasa & Roughgarden 1984). Recent studies, though, have challenged this proposition. Campbell & Grime (1989a, b; Campbell *et al.* 1992) demonstrated that fast-growing plants are able to forage equally well below ground (for mineral nutrients and water) and above ground (for light). This suggests that the very nature of a plant having a high growth rate applies equally to roots and shoots (Grime *et al.* 1997), and that faster-growing plants are better competitors for available resources both below and above ground because they are able to forage and acquire both types of resources at a higher rate.

A further complication is that several below-ground resources can be limiting. In herbaceous wet vegetation biomass production is most frequently limited by nitrogen or phosphorus (Koerselman *et al.* 1990; Verhoeven *et al.* 1993, 1996; Bakker & Olff 1995). Which of the two nutrients is limiting does not so much depend upon their absolute supplies, but on their relative supplies, as indicated by the biomass N:P ratio (Verhoeven *et al.* 1996). N-limitation and P-limitation are generally found in plant communities with different species composition (Bedford *et al.* 1999; Roem & Berendse 2000). This suggests that plant species differ in their abilities to compete under N- and P-limitation, which according to Tilman (1982, 1997) is due to differing abilities to tolerate low supplies of N and P. Again the question arises whether these abilities are positively or negatively correlated across plant species.

There is an absence of experimentally derived comparative data sets illustrating relationships between the abilities of a set of wetland plants to tolerate low nitrogen, low phosphorus and low light. We therefore set out to generate this data for a set of well-stud-

Table 1. *Wetland plant species used in the experiment, with their average biomass in the control treatment (g dry weight), their relative performance (average biomass of low-resource treatment divided by average biomass of control) under low light (L), nitrogen (N), and phosphorus (P), and the results of ANOVAs testing the significance of differences among the three low-resource treatments for each species. Nomenclature follows Gleason & Cronquist (1991)*

Species	Abbr	Biomass	Relative performance			Anova results	
		Control	Low L	Low N	Low P	*F*-ratio	*P*
Acorus calamus	Acal	3.12	0.076	0.288	0.158	19.98	<0.001
Asclepias incarnata	Ainc	9.63	0.417	0.169	0.112	47.25	<0.001
Bidens cernua	Bcer	13.73	0.237	0.146	0.255	5.57	0.016
Carex crinita	Ccri	2.72	0.559	0.438	0.559	0.93	0.421
Coreopsis rosea	Cros	2.16	0.047	0.356	0.000	133.42	<0.001
Cyperus aristatus	Cari	6.81	0.200	0.250	0.707	26.41	<0.001
Cyperus rivularis	Criv	8.77	0.072	0.173	0.257	8.65	0.003
Echinochloa wiegandii	Ewie	10.69	0.674	0.178	0.404	117.60	<0.001
Eleocharis calva	Ecal	9.83	0.053	0.207	0.516	76.32	<0.001
Epilobium ciliatum	Ecil	8.43	0.211	0.206	0.413	9.19	0.002
Glyceria canadensis	Gcan	5.43	0.127	0.181	0.279	3.48	0.058
Lythrum salicaria	Lsal	14.37	0.133	0.143	0.438	104.07	<0.001
Panicum longifolium	Plon	1.38	0.102	0.606	0.113	58.92	<0.001
Phalaris arundinacea	Paru	15.36	0.350	0.114	0.392	8.786	0.003
Rumex verticillatus	Rver	14.25	0.414	0.117	0.346	22.31	<0.001
Scirpus americanus	Same	4.94	0.080	0.217	0.374	18.16	<0.001
Scirpus validus	Sval	11.35	0.048	0.141	0.274	9.66	0.002
Solidago galetorum	Sgal	4.35	0.028	0.216	0.037	11.17	0.001
Spartina pectinata	Spec	14.79	0.109	0.137	0.215	11.60	0.001
Typha glauca	Tgla	8.80	0.110	0.174	0.000	6.88	0.025
Verbena hastata	Vhas	11.71	0.320	0.121	0.257	7.05	0.007

ied wetland species (e.g. Shipley & Peters 1990; Boutin & Keddy 1993) that occur along strong fertility gradients and that are known to compete vigorously, at least under fertile conditions. We ask three questions. (1) Do plants of different positions along fertility gradients differ in their ability to tolerate low resource levels? (2) Are there trade-offs? Do plants that tolerate low P tend to be less able to tolerate low N? Or do plants that tolerate low nutrient supply tend to be less able to tolerate low light availability? (3) Is tolerance of low resource levels as measured in this study correlated with published data on the competitive abilities of the same species?

Methods

We compared the responses of 21 wetland plant species (Table 1) to shortages of three essential resources: light, phosphorus and nitrogen. The plants were grown over one growing season in a 100-m^2 outdoor compound at Carleton University, Ottawa,

Canada (45° 25' N, 75° 45' W). It is essential, when looking for general relationships among plant traits, to evaluate many species simultaneously (Grime 1979; Tilman 1988; Keddy 1992). Therefore, we used wetland species of contrasting ecology from a wide range of natural habitats (Table 1).

Seeds of the 21 species had been collected from across eastern Canada (Nova Scotia to Ontario) and overwintered at 2 °C in damp sand. They were germinated on plain sand in 1-l plastic pots and then grown singly in these pots for the duration of the experiment. In the control pots, 35 ml of Hoagland's nutrient solution was added to the pots one week after germination, and 50 ml of a triple-strength solution was added weekly thereafter for 16 weeks. Low-nutrient treatments received 35 ml of 1/10 strength Hoagland's on a weekly basis for the first four weeks, and after four weeks received 50 ml of Hoagland's solution (full strength but lacking either nitrogen or phosphorus) every week for 13 weeks. Thus, the total amounts of N and P received by a plant were 510.86 mg and 75.73 mg in the control treatment, 139.31 mg and 0.44 mg in the low-P treatment, and 2.94 mg and 20.66 mg in the low-N treatment. Plants designated for the shade treatment were covered with 65% shade cloth after three weeks, 80% in the next week and 90% after three more weeks. Due to mortality of seedlings some transplanting was necessary. Seedlings for transplanting were obtained from experimental pots where more than one plant had germinated or from other pots which had a one part organic/three part sand mixture. Most transplanting was done in the first two weeks of the experiment, although transplanting of four species (*Lythrum salicaria, Solidago galetorum, Rumex verticullata* and *Glyceria canadensis*) was performed four weeks into the experiment.

Plants were grown for 17 weeks, and placed in a randomized design with six replicates per treatment. They were then harvested and total (above- and below-ground) biomass was measured for each plant. Relative performance in each low-resource treatment was calculated as biomass of plants grown in treatment divided by plants grown in control. The rationale for using relative rather than absolute performance is that not all plants have the same inherent body size; if this was not accounted for, the larger plants would appear to be better stress tolerators just because they are bigger.

A one-way ANOVA was used to determine if there were differences in the total biomass of the plants (pooling all species) among the four treatments, followed by Tukey's Honestly Significant Difference test to separate the treatment means. For each species, differences in relative performance among the three low-resource treatments were tested with ANOVA followed by Tukey's Honestly Significant Difference test to ascertain whether species responded differently to different resource constraints. Pearson's correlation analysis was used to determine whether the relative performance of the 21 species under each of the three low-resource levels was correlated with their biomass in the control treatment (log-transformed) and with their relative performance under one of the other low-resource levels. For part of the species, Pearson correlation coefficients were also calculated for the relationship between relative performance under each of the three low-resource levels and competitive effects (ten species, data from Gaudet & Keddy 1995) or competitive responses (sixteen species, data from Keddy *et al.* 1998). Competitive effect was measured as the percentage reduction in biomass of a common phytometer, *Lythrum salicaria,* when surrounded by the test species,

compared to phytometers grown alone (based on data from Gaudet & Keddy 1988, 1995). Competitive response was measured as the percentage reduction in biomass of the species when grown from seedling under an established canopy compared to plants grown alone (Keddy *et al.* 1998). Lower values indicate that there is little difference in biomass between grown alone and grown with neighbours, i.e. a high competitive response.

Results

The low resource levels had a major effect on plant growth. Across all species, the average biomass production in treatments was significantly decreased relative to the control (ANOVA, F-ratio 172.232, $P < 0.001$). The low nitrogen treatment had the greatest overall effect on biomass production, and phosphorus had the least (Figure 1).

Most of the 21 species were considerably affected by the low-resource treatments (Table 1). Among the 21 species, low light had the greatest effect (in descending order) on *Solidago galetorum, Scirpus validus* and *Coreopsis rosea* and the least effect on *Echinochloa wiegandii, Carex crinita* and *Asclepias incarnata.* Low nitrogen had the greatest effect on *Phalaris arundinacea, Rumex verticillatus* and

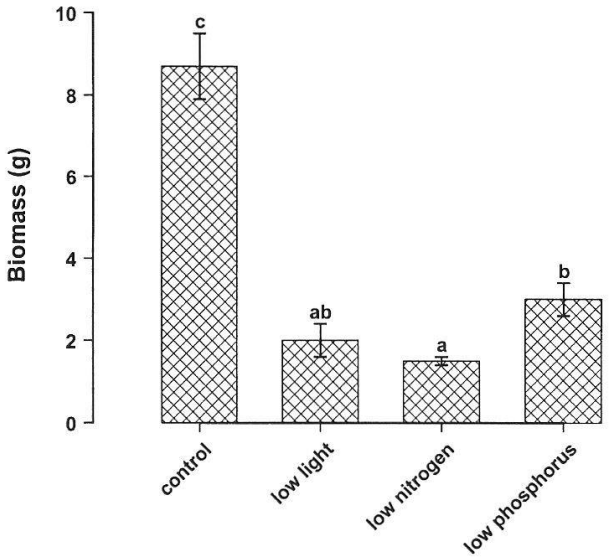

Fig. 1. *Effect of low resource levels on the mean biomass of the 21 test species. Bars sharing the same letter are not significantly different (Tukey's HSD). Error bars represent 95% confidence limits.*

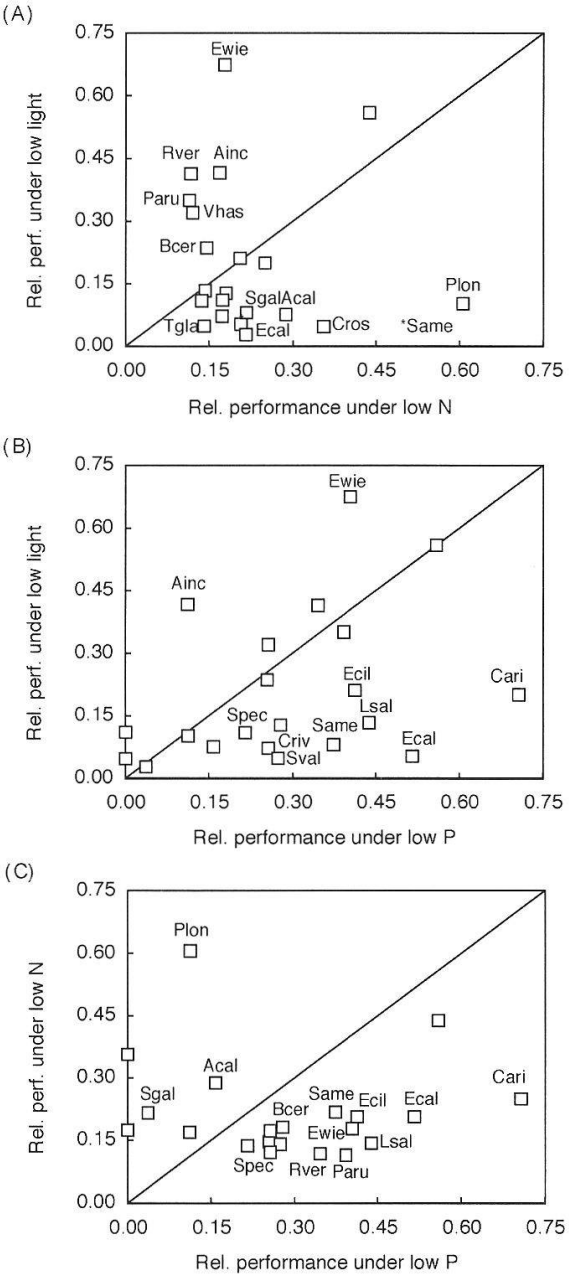

Fig. 2. *Relationships between the relative performance of species (a) under low light and low nitrogen; (b) under low light and low phosphorus; and (c) under low nitrogen and low phosphorus. Species with statistically significant differences in performance between pairs of treatments (Tukey's HSD, $P < 0.05$) are indicated by displaying species abbreviations (see Table 1) beside symbols.*

Verbena hastata and the smallest effect on *Panicum longifolium, Carex crinita* and *Coreopsis rosea.* Low phosphorus had the greatest effect on *Coreopsis rosea, Typha glauca* and *Solidago galetoreum* and the smallest effect on *Cyperus aristatus, Eleocharis calva* and *Carex crinita* (Table 1).

Most species performed significantly better in any one of the three low-resource treatments, i.e. were not affected by low supply of different resources to the same extent (Table 1, Fig. 2). The only two exceptions were *Carex crinita* and *Glyceria canadensis* (Table 1). The largest differences in relative performance be-

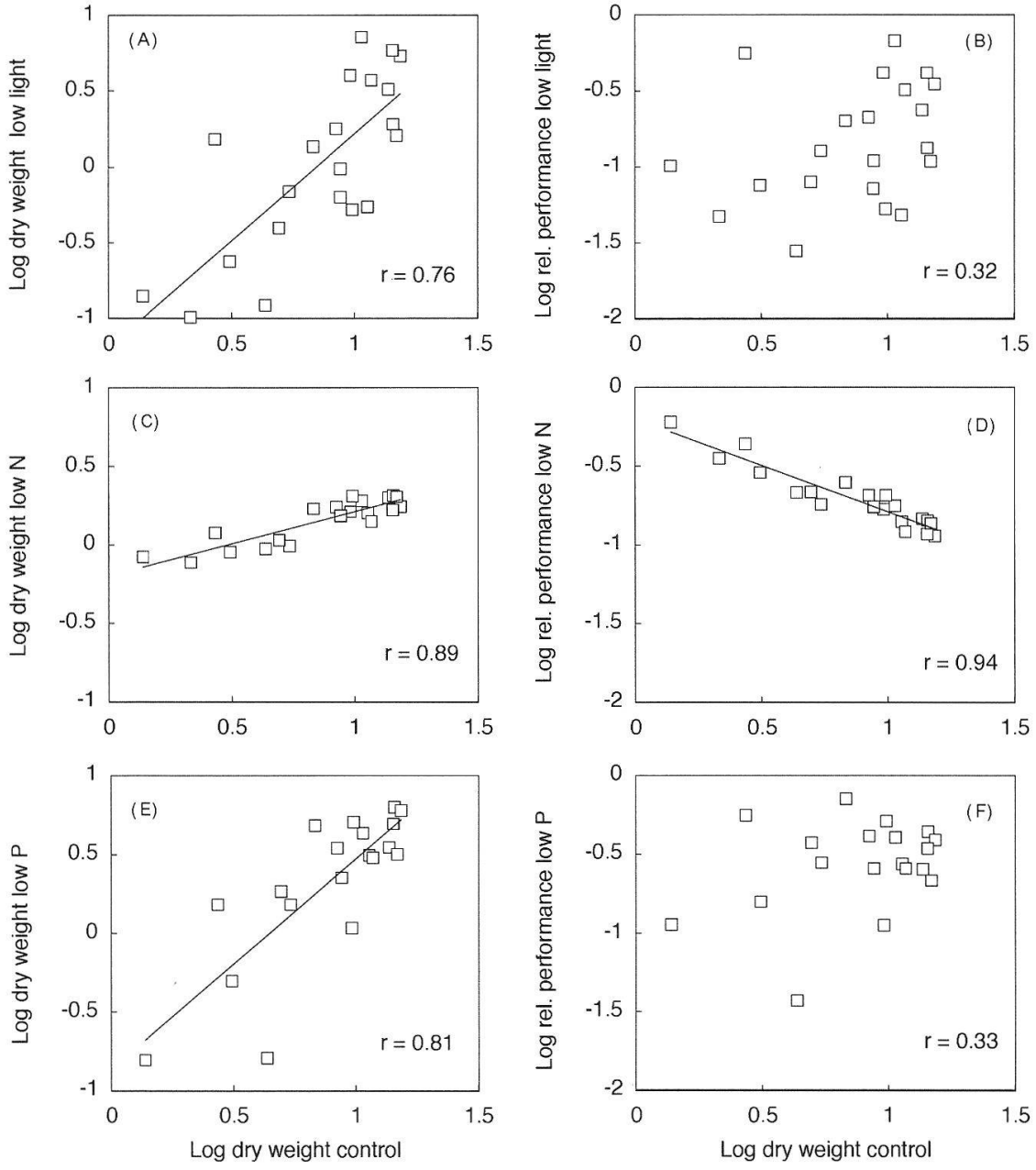

Fig. 3. *Relationships between the performance of species under (a, b) low light, (c, d) low nitrogen, and (e, f) low phosphorus and their biomass under high resource supply (control treatment). Performance under low resource supply was measured (a, c, e) as biomass (g dry weight) and (b, d, f) as relative performance (biomass under low resource supply divided by biomass under high resource supply). All variables were log-transformed.*

Table 2. *Correlations between the relative performance of plant species under low resource supply (data from this study), competitive effect (from Gaudet & Keddy 1988), and competitive response (from Keddy* et al. *1998), given as Pearson correlation coefficients* (r)

	Relative performance under		
	Low L	Low N	Low P
Relative performance under low N	0.073		
Relative performance under low P	-0.361	0.101	
Competitive effect	0.099	-0.762	0.200
Competitive response	-0.376	0.674	0.016

tween low-resource treatments were found in *Echinochloa wiegandii* and *Panicum longifolium* (comparing low N and low light; Fig. 2a), *Echinochloa wiegandii, Asclepia incarnata, Cyperus aristatus,* and *Eleocharis calva* (comparing low P and low light; Fig. 2b), and *Panicum longifolium* and *Cyperus aristatus* (comparing low N and low P; Fig. 2c).

Correlation analysis showed that if absolute biomass values were considered, the biomass of the 21 species under low resource supply was strongly positively correlated with their biomass under high resource supply (control treatment; Fig. 3a, c, e). By contrast, relative performance under low resource supply was negatively correlated (low N) or uncorrelated (low light, low P) with the species' biomass in the control treatment (Fig. 3b, d, f). The reason for this difference was that biomass under low N increased less than proportionally with increasing control biomass (Fig. 3b), whereas biomass under low light or low P increased more than proportionally (Fig. 3a, c). In other words, biomass under low N varied much less among the 21 species (coefficient of variation $CV = 0.29$) than biomass under low light ($CV = 1.05$) or under low P ($CV = 0.75$). Relative performance under low light had little correlation with performance under low N or low P. Performance under low N, likewise, was not well correlated with performance under low P (Table 2, Fig. 2). Performance under low light was not significantly correlated with competitive effect (Fig. 4a), nor was performance under low P (Fig. 4c). However, performance under low N was negatively correlated with competitive effect (Fig. 4b). Performance under low light was not significantly correlated with competitive response (Fig. 5a), nor was performance under low P (Fig. 5c), whereas performance under low N was positively correlated with competitive response (Fig. 5b).

Discussion

The purpose of this study was to test two predictions derived from Tilman's (1982, 1988, 1997) competition theory. Therefore, it is important to note that this was not a competition study. The experimental low-resource conditions resulted from reduced resource supply to the experimental units (pots), and not from competitive interactions. Therefore, the comparative performance of species under low resource supply may have differed somewhat between this experiment and natural vegetation, where competition occurs. The experimental treatments, though, were not unrealistic. Plants face many growth constraints in most natural habitats, and often there is a large imbalance in the availability of essential resources, leading to strong limitation by one particular resource (e.g. Verhoeven *et al.*

1996). Experiments similar to ours have also been used by Tilman to validate his theory (e.g. Tilman *et al.* 1999)

The resources that were systematically limited in this experiment (light, nitrogen and phosphorus) all proved to significantly reduce the biomass of the test species compared to the "non-limited" conditions in the control treatment (Fig. 1). Phosphorus, though, was significantly less of a constraint on biomass

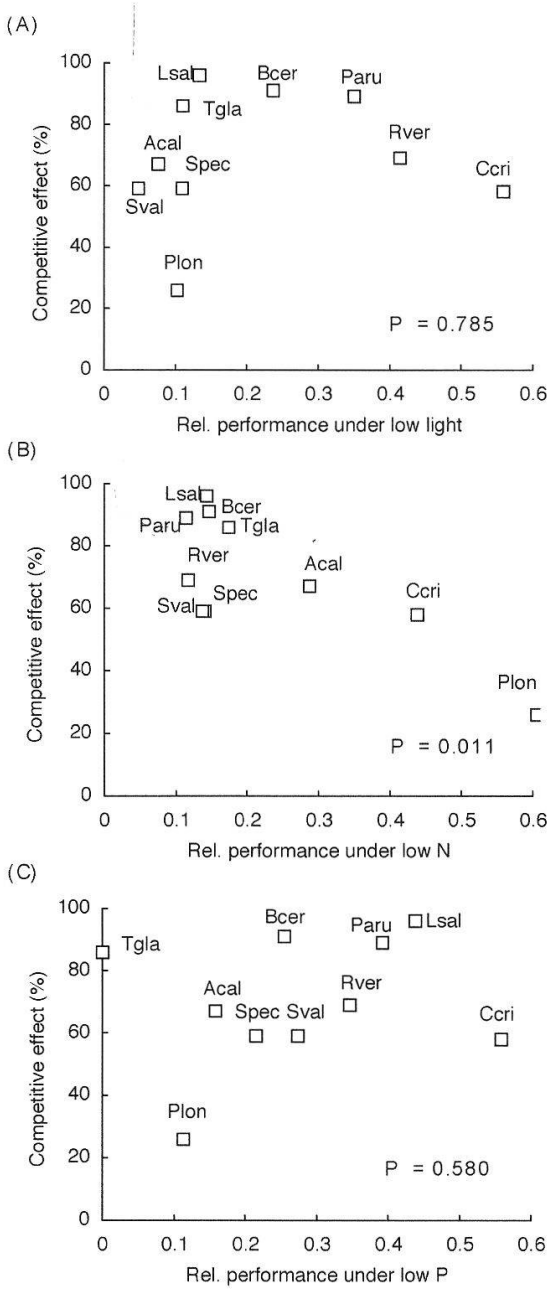

Fig. 4. Relationships between the competitive effect of species (Gaudet & Keddy 1988, 1995) and their relative performance under (a) low light, (b) low nitrogen, and (c) low phosphorus. A species with high competitive effect value had a high ability to suppress the phytometer Lythrum salicaria.

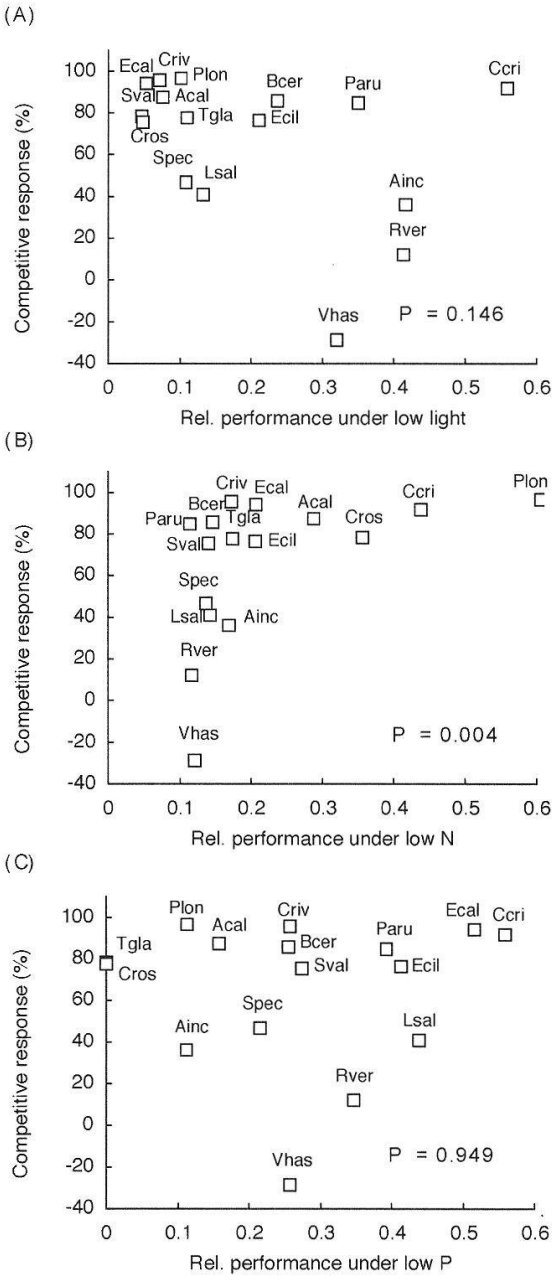

Fig. 5. Relationships between the competitive response of species (Keddy et al. *1998) and their performance under (a) low light, (b) low nitrogen, and (c) low phosphorus. A low competitive response value indicates that there was little difference in biomass between plants grown alone and those grown under an established canopy, i.e. that the species responds well to competition.*

than nitrogen in this experiment. This difference may have two causes. First, the river sand used in the experiment probably contained a non-negligible amount of phosphorus, but little nitrogen. Fertilization experiments in early-successional vegetation on sand regularly showed nitrogen to be the limiting nutrient (Willis 1963; Olff *et al.* 1993) due to the relatively high P-content of the sand (Olff *et al.* 1993). Second, the complete Hoagland solution supplied during the first four weeks of the experiment provided plants with more phosphorus than nitrogen relative to their needs. The N:P ratio of the Hoagland solution was approximately 7, whereas plants need N and P in a ratio of approximately 10–15. Based on these ratios, it could be expected that the amount of P supplied in the low-phosphorus treatment would allow plants to produce up to twice as much biomass as the amount of N supplied in the low-nitrogen treatment, which is in good agreement with the results. For individual species, the phosphorus content of seeds may also have been an important source of phosphorus (Köhler *et al.* 2001).

The general reduction in biomass due to resource limitation allowed us to further analyze how different plant species responded to the different resource constraints and to examine whether there is a significant and predictable relationship between the performance of species under low levels of different resources. According to Tilman's resource ratio hypothesis (1982, 1988), the species that can tolerate the lowest levels of a resource is the best competitor for that resource. Furthermore, Tilman proposes that a good competitor for below-ground resources cannot be a good competitor for above-ground resources, and vice-versa, because of a trade-off in the allocation of biomass to above- or below-ground resource acquisition. Based on this logic, plants that are good performers under low light should be poor performers under a low-nutrient condition (but see Donald 1958; Thompson 1987; Grime *et al.* 1997 for contrasting opinions).

Our results do not support Tilman's theory. We found no negative correlation between relative performance under low light and relative performance under either of the two low-nutrient treatments (Table 2). Only the responses of *Panicum longifolium,* performing well under low nitrogen and poorly under low light, and of *Echinochloa wiegandii,* performing poorly under low nitrogen and well under low light, were consistent with Tilman's hypothesis, whereas the other 19 species did not show such a trade-off. A number of species performed quite well under low phosphorus and poorly under low light, but an equal number performed poorly both under low phosphorus and under low light. These results do not support Tilman's hypothesis, but they do not support the alternative model proposed by Grime (1977, 1979) either. According to Grime's CSR-model, plant species can be ranked on a common axis of stress tolerance based on traits such as growth rate, life span etc. This model suggests a positive correlation between the performance of species under low light and under low nutrient supply, which is at variance with our results.

If the ability of species to tolerate low nutrient supply was determined by biomass allocation to roots, as assumed by the resource ratio hypothesis, there should be a positive correlation between the performance of species under low nitrogen and low phosphorus. No correlation was found in this study, i.e. plants able to tolerate low nitrogen levels could not necessarily tolerate low phosphorus levels. This strongly suggests that interspecific differences in the response to low nutrient supply are not simply due to differences in biomass

allocation, but due to more complex, nutrient-specific mechanisms. Assuming that in our experiment, some phosphorus was present in the river sand, the ability of the species to solubilize and take up this phosphorus would be decisive for their performance under low P supply (cf. Perez-Corona *et al.* 1996; Aerts & Chapin III 2000). Other mechanisms are for example mycorrhizal infection, nutrient allocation within the plant or nutrient resorption, which have different effects on the nitrogen and phosphorus economy of the plants, and which all vary considerably among species (Wetzel & van der Valk 1996; Aerts & Chapin III 2000). In addition, as mentioned above, the low-nitrogen and the low-phosphorus treatment differed in the degree to which they restricted plant growth in this study, and this may also have contributed to the different species rankings.

Performance under low nitrogen was significantly correlated with competitive effect (Fig. 4b) and with competitive response (Fig. 5b). Formally, the relationships were opposite: species that performed well under low nitrogen had low competitive effect values, but high competitive response values. However, since low values for competitive response indicate high competitive ability, the relationships actually both indicate that competitive ability was negatively related to performance under low nitrogen supply. This contrasts with Tilman's (1982, 1988) resource ratio hypothesis, which predicted a positive relationship, whereas it is basically consistent with Grime's (1977, 1979) CSR model, which assumes a trade-off between stress tolerance and competitive ability. However, given the strong negative correlation between performance under low nitrogen and biomass under high resource supply (Fig. 3d), it could be that the negative correlation found between performance under low nitrogen and competitive ability in this study only reflected a positive correlation between biomass under high resource supply and competitive ability (Gaudet & Keddy 1988). Thus, our results do not indicate whether there is any direct (causal) relationship between tolerance of nitrogen stress and competitive ability.

Performance under low phosphorus and low light did not correlate with either competitive effect or competitive response. The most obvious explanation is that neither performance under low phosphorus nor performance under low light correlated with control biomass in our study, and that correlations between relative performance under low resource supply and competitive ability are actually determined by correlations of both variables with biomass under high resource supply. Alternatively, the lack of correlation might be related to the experimental conditions under which values for competitive effects and responses were determined. In both experiments, the substrate and fertilizer used (Gaudet & Keddy 1988; Keddy *et al.* 1998) indicate that plant growth was primarily limited by nitrogen. Since we have found that the performance of species under different resource constraints does not correlate, the same is likely to hold for the competitive abilities of species when growth is limited by different resources. It would be of great interest to compare the species rankings found in this study with values for competitive effects and responses determined under clearly phosphorus- or light-limited conditions. If correlations were found to be resource-specific, they would provide some evidence for a direct relationship between tolerance of low resource supply and competitive ability. Another possibly important factor is that values for competitive effects and responses (Gaudet & Keddy 1988, 1995; Keddy *et al.* 1998) were determined in short-term

experiments, as was the case for performance under low resource supply (this study). It would also be interesting to compare performance under low resource supply with competitive effect and competitive response determined in longer-term experiments. This would allow a more direct test of predictions derived from Tilman's resource ratio hypothesis since the latter is concerned with the long-term outcome of competition.

Conclusions

There is a wide variation between species in their performance under all three of the low resource treatments. This suggests that different species have quite different resource requirements for their growth and survival. However, we found no trade-offs between abilities to tolerate low N, low P or low light. Success with which we can predict the comparative performance of species under low resource supply based on comparative data on competitive response and competitive effect is inconclusive. The results of this study suggest that it may be important to distinguish among nitrogen-, phosphorus- and light-limited conditions when testing relationships between performance under low resource levels and competitive ability.

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