

Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments?

PAUL A. KEDDY, LISA TWOLAN-STRUTT and IRENE C. WISHEU
Biology Department, University of Ottawa, Ottawa, Ontario, Canada K1N 6N5

Summary

1 There is evidence that plants in natural communities form transitive competitive hierarchies, but the pervasiveness and malleability of hierarchies remain controversial. We constructed three competitive rankings among 20 wetland plant species in conditions known to be important in wetlands: a mesic, fertile environment, an infertile environment and a flooded environment.

2 Rankings were constructed using plants grown from seed in pairwise combinations for one growing season in an outdoor compound. The indicator species used to construct the rankings were *Carex crinita*, *Gnaphalium uliginosum* and *Lycopus americanus*. The others represented a wide array of morphologies, habitats and abundances and ranged from the large cosmopolitan *Typha angustifolia* to the small and rare *Sabatia kennedyana*.

3 Competitive rankings formed in all three environments. Competitive effect rankings based upon the results for all three indicator species were significantly concordant across the three environments ($W = 0.59$; $P < 0.05$), i.e. competitive effect did not change across environment. When calculated separately for each indicator species, rankings across the three environments were significantly concordant for two of the three indicator species. Within any environment the ranking varied among the indicator species.

4 Rankings based upon the mean competitive response to all three phytometer species were not concordant across the three environments ($W = 0.35$; $P > 0.3$) and were not concordant when calculated separately for each indicator species. Within any environment, response rankings were significantly concordant for two out of the three indicator species.

5 Competitive effect rankings tended to be constant across environments and were sensitive to the kind of neighbour. Competitive response rankings varied across environments and were insensitive to the kind of neighbour.

Keywords: competition, competitive performance, flooded environment, hierarchies, infertile environment

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Introduction

It is more than 60 years since Clements published his landmark work on competition (Clements *et al.* 1929) and yet fundamental questions about competition remain unanswered. Important unresolved questions include: (1) are communities organized into competitive hierarchies and if so (2) do these hierarchies vary among environments? Recent reviews suggest that the answer to the first question is yes (Keddy & Shipley 1989; Shipley 1993; Shipley & Keddy 1994). The second question is related to whether and how

competition varies among environments which is one of the most divisive debates in plant competition (e.g. Grime 1977; Grime 1979; Tilman 1982; Tilman 1988; Campbell *et al.* 1991; Grace 1991). One reason for the lack of agreement is the trade-off inherent in the design of competition studies (Fig. 1). A vast majority of published studies have looked at a few species in one or two environments. Owing in part to the importance of the foregoing two questions, plant ecologists have recently tried to increase either the number of species or the number of environments. In this paper we try for the middle path of exploring com-

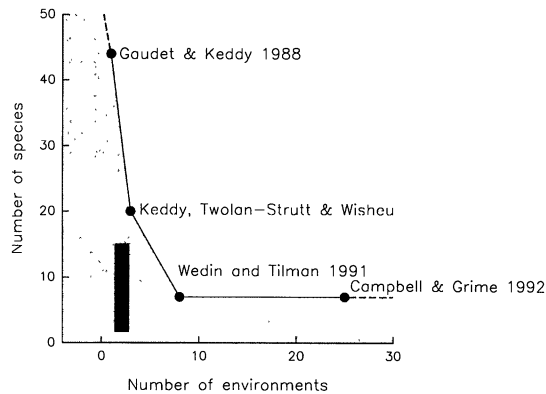


Fig. 1 Limits of the experimental study of plant competition. There is an inherent trade-off between the number of pairs of species and the number of environments examined. We have plotted only studies which appear to define the edges or limits of the species/environments envelope. A majority of existing studies involve 1–15 species in one or two environments (solid area).

petitive rankings among 20 species in three different environments: a control environment – a mesic, fertile situation typical of many wetlands, a low fertility wetland environment and a flooded environment.

To explore competitive rankings of species, we must consider what is meant by competitive ability. ‘Competitive ability’ has two components (Goldberg 1990): competitive effect (the ability to depress the growth or reproduction of neighbours) and competitive response (the ability to withstand the negative effects of neighbours). These can both be estimated by growing species in additive mixtures and measuring the reduction in performance of species in mixtures relative to controls. Making such comparative measures on large numbers of species simultaneously is one of several possible research strategies in plant ecology (Keddy 1992). In this study we rank 20 species with respect to these two components and pose four questions.

- 1 Do relative competitive effect and response rankings differ among three different environments?
- 2 Do relative competitive effect and response rankings vary among three indicator species, *Carex crinita*, *Gnaphalium uliginosum* and *Lycopus americanus*, which differ in morphology and habitat preference and belong to different wetland guilds?
- 3 Are relative competitive effect and response correlated among environments?
- 4 Is relative competitive effect correlated with relative competitive response in each environment?

For the sake of clarity, there are two subsections of the paper: a competitive effect section and a competitive response section. Only at the end are they combined.

Methods

SPECIES

A guiding principle in choosing species for this study was the inclusion of wetland plants having a wide

range of morphology, life history and habitat. The twenty wetland species chosen represent seven functional groups (Keddy 1990; Boutin & Keddy 1993) (Table 1), occur in a wide range of natural habitats including lake shores, marshes and floodplains and include plants ranging from mudflat annuals (e.g. *Gnaphalium uliginosum*) to long-lived clonal dominants (e.g. *Typha angustifolia*), and from dangerous invasive exotics (e.g. *Lythrum salicaria*) to nationally threatened species (e.g. *Sabatia kennedyana*).

EXPERIMENTAL DESIGN

An additive design was used in which three indicator species, *Carex crinita* (interstitial tussock), *Gnaphalium uliginosum* (ruderal obligate annual) and *Lycopus americanus* (ruderal facultative annual), were grown in all possible pairwise mixtures with each other and with 17 neighbour species. Each of the 20 species was also grown alone. All pairs and single plants were grown under three sets of environmental conditions: control, flooded and infertile. This was replicated five times using a randomized block design. A total of 1110 pots were used in the experiment with 222 pots in each of the five blocks. Within each block, seventy four pots represented each environment. Fifty four of these contained plant pairs and 20 contained single plants. This design yielded 20 estimates of mean plant yield with three different indicator species under three sets of conditions.

EXPERIMENTAL PROCEDURE

The experiment was run in an outdoor compound at Carleton University, Ottawa, Canada (45°25'N, 75°45'W) from May to September of 1989. Seeds were collected across Eastern North America during the years 1987–89 and stored at 4 °C. The seeds were sown on May 3 in plastic flats and covered with shade cloth. Germination for 15 species occurred in the second week and the remaining 5 species germinated during the third and fourth weeks. From 12 to 15 June, seedlings were planted in unshaded 6-cm-diameter pots containing a mixture composed of one part organic soil, one part sand and one part peat. These pots were placed inside 10 cm collar pots which contained drainage holes.

Plants in the control and flooded environments were hand watered daily and were fertilized every 12 days with 7 mg N; 11 mg P, 27 mg K and 17 mg calcium nitrate per pot (7:11:27 N–P–K and 15:0:0 calcium nitrate mixtures, B & B Hydroponics, Ottawa, Canada). Drainage holes in the collar pots for this treatment were at ground level to prevent accumulation of water, but in the flooded treatment drainage holes were at soil level. Plants in the infertile environment were treated as the controls, except that plants were fertilized with a solution ten times less concentrated. The roots and shoots of plants were harvested

Table 1 Twenty wetland species used in the experiment (nomenclature follows Gleason 1952; guilds follow Boutin & Keddy 1993)

| Species | Guild | Code |
|---|--------------------------------|------|
| <i>Hypericum ellipticum</i> Hook. | Interstitial clonal | HE |
| <i>Eleocharis erythropoda</i> Steud. | Interstitial reed | EE |
| <i>Juncus filiformis</i> L. | Interstitial reed | JF |
| <i>Acorus calamus</i> L. | Interstitial tussock | AC |
| <i>Carex crinita</i> Lam. | Interstitial tussock | CC |
| <i>Eupatorium maculatum</i> L. | Interstitial tussock | EM |
| <i>Scirpus cyperinus</i> (L.) Kunth. | Interstitial tussock | SC |
| <i>Sparganium eurycarpum</i> Engelm. | Matrix clonal dominant | SE |
| <i>Typha angustifolia</i> L. | Matrix clonal dominant | TA |
| <i>Gratiola aurea</i> Pursh. | Matrix clonal stress tolerator | GA |
| <i>Panicum longifolium</i> Torr. | Matrix clonal stress tolerator | PL |
| <i>Sabatia kennedyana</i> Fern. | Matrix clonal stress tolerator | SK |
| <i>Eleocharis obtusa</i> (Willd.) Schult. | Ruderal facultative annual | EO |
| <i>Lycopus americanus</i> Muhl. | Ruderal facultative annual | LA |
| <i>Lythrum salicaria</i> L. | Ruderal facultative annual | LS |
| <i>Mimulus ringens</i> L. | Ruderal facultative annual | MR |
| <i>Verbena hastata</i> L. | Ruderal facultative annual | VH |
| <i>Cyperus aristatus</i> Rottb. | Ruderal obligate annual | CA |
| <i>Gnaphalium uliginosum</i> L. | Ruderal obligate annual | GA |
| <i>Juncus bufonius</i> L. | Ruderal obligate annual | JB |

from 18 September to 19 October, dried for a minimum of 24 hours and their total biomass weighed. Any plants that died before 21 July were replaced and those dying after this date were included in the analysis as plants with final biomass equal to zero. Plants which had been grazed or had dropped leaves prior to harvest were excluded from the analysis.

ANALYSIS

Mean total biomass of the indicator species and of the neighbour species was calculated for each environment. The Kruskal–Wallis test was used to test for differences in phytometer biomass and neighbour species biomass among the three environments. Non-parametric multiple comparisons were used to determine among which environments the mean biomass differed (Zar 1984). The relative yield per plant was calculated for each species in each replicate of each environment using the following equation

$$RYP_{ij} = Y_{ij}/Y_i,$$

where RYP_{ij} is the relative yield per plant of species i in interaction with plant species j , Y_{ij} is the yield of an individual of species i grown with an individual of species j and Y_i is the yield of an individual of species i grown alone (Harper 1977). Our measures of relative yield are based on an additive design, not a replacement series design. Some relative yield values were greater than 1 meaning that some plants had greater biomass when grown with a neighbour than when grown alone. These positive, commensal interactions between plants occurred with low frequency in the three treatments and were included in the analysis.

Mean relative yield per plant species was then calculated for all indicator species and all neighbour species. These mean relative yield values were used to establish one effect and one response matrix for each of the three environments. The effect matrices include the mean effect of each neighbour species on each indicator species (the ability of each neighbour species to damage each indicator species), mean effect of each neighbour species on all indicator species (row means of matrix) and the mean effect of all neighbour species on each indicator species (column means of matrix). Similarly the response matrices include mean response of each neighbour species to each indicator species (the ability of each neighbour species to withstand the effects of each indicator species), mean response of each neighbour species to all indicator species (row means of matrix) and the mean response of all neighbour species to each indicator species (column means of matrix). Species within each effect and response matrix were ranked from 1 to 20 and 1 to 17, respectively, with 1 corresponding to the species with highest competitive performance (i.e. a neighbour species with a low mean competitive effect value or high mean competitive response value). Kendall's coefficient of concordance (Siegel 1956) was used to test for concordance of rankings of competitive effect and response among environments and among phytometer species. Bivariate correlation was used to determine the intensity of association between the mean relative effect of species in different environments and between the mean relative response of species in different environments. It was also used to explore the relationships between mean relative effect and response of plants in each treatment.

Competition intensity was calculated for each rep-

licate of each pairwise interaction between two species using the following equation

$$I = (1 - RYP_{ij}) + (1 - RYP_{ji}),$$

where I is the intensity of the interaction between species i and j . The mean competition intensity was then calculated for each environment. The Kruskal–Wallis test was used to test for differences in mean competition intensity among the three environments. Statsgraphics Version 3.0 (Statsgraphics 1988) and SAS Version 6.02 (SAS 1987) were used to carry out these analyses.

Results

PLANT GROWTH AND COMPETITION INTENSITY

Mean biomass of both the indicator and neighbour was less under infertile conditions than in the control environment ($P < 0.001$ in both cases) and flooded environment ($P < 0.001$ in both cases), the latter two not being different (Fig. 2a,b). Mean competition intensity did not differ among plants in the three environments ($P = 0.11$) (Fig. 2c). Raw data are available from the authors.

COMPETITIVE EFFECT

The competitive effects of the 20 plant species were significantly correlated among environments (Fig. 3) resulting in species rankings that were significantly concordant across the three environments ($W = 0.59$, $\chi^2_{19} = 33.6$, $P < 0.05$) when these rankings were calculated from the mean results of the three indicator species. When separated by species, the rankings were concordant when *Carex crinita* and *Gnaphalium uliginosum* were used as indicator species, but were not significantly concordant across the three indicator species within any environment (Table 2).

COMPETITIVE RESPONSE

No significant correlations were found between relative competitive responses in different environments (Fig. 4). Rankings were also not significantly concordant across the three environments ($W = 0.35$, $\chi^2_{14} = 16.8$, $P > 0.3$; rankings were calculated from the mean results for the three indicator species). When separated by indicator species, the rankings were not concordant across environments for any of the three species (Table 3). However, these rankings were concordant across indicators within the control and the flooded environments. The results were reanalysed excluding the competitive response of *Juncus filiformis* and *Hypericum ellipticum* which were obvious outliers in Fig. 3. When this was done, the results of the correlation analyses and the test of concordance based on the mean of the indicator species remained the

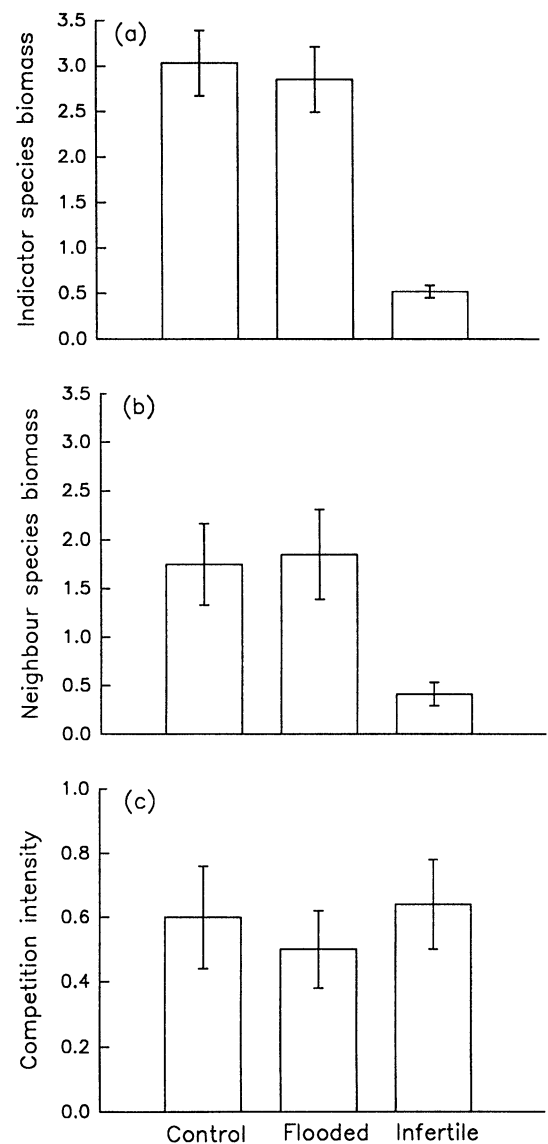


Fig. 2 (a) Mean biomass of three indicator species grown alone and in interaction. (b) Mean biomass of the 17 neighbour species grown in alone and in interaction. (c) Intensity of competition between plants in the three environments.

same. When the concordance tests for the individual indicator species were repeated, competitive response was no longer concordant across indicator species in the flooded environment.

EFFECT AND RESPONSE

Relative competitive effect and response were not significantly correlated in any of the environments (Fig. 5). These results were the same when *Juncus filiformis* and *Hypericum ellipticum* were excluded from the analysis.

Discussion

LIMITATIONS OF EXPERIMENT

How much can we infer from short-term studies of seedlings? The recruitment stage is important in many

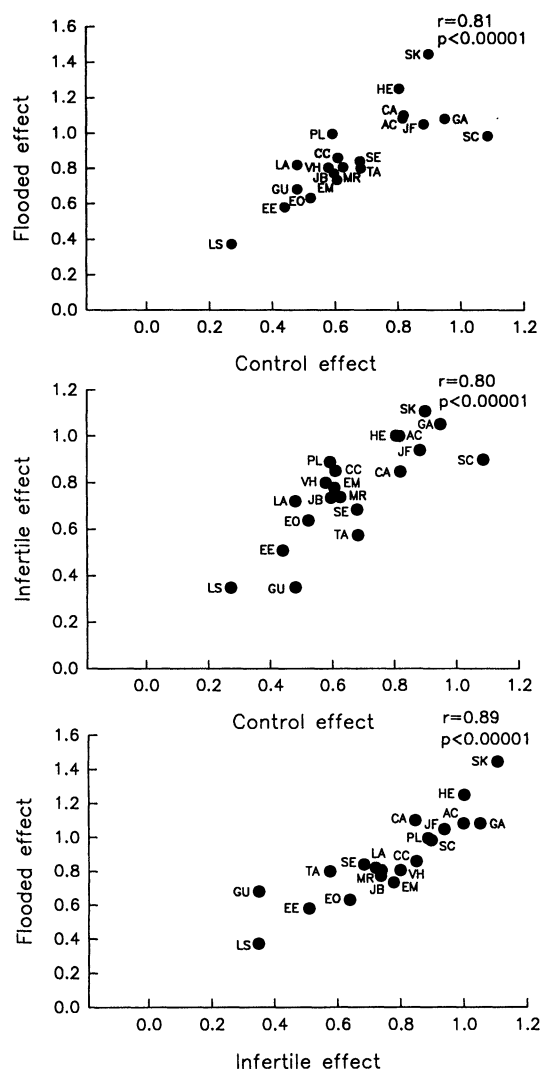


Fig. 3 Correlations among mean relative competitive effect for $n = 20$ species in three environments.

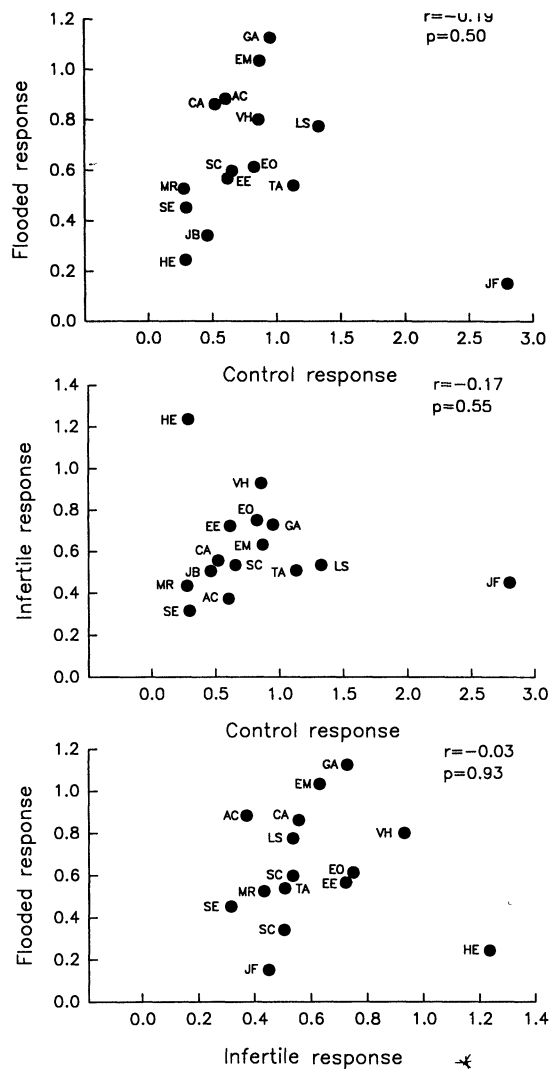


Fig. 4 Correlations among mean relative competitive response for $n = 17$ species in three environments.

vegetation types (Grubb 1977), and we know that periodic mass regeneration from seed occurs in some wetlands during low water periods (van der Valk 1981; Keddy & Reznicek 1982; Leck *et al.* 1989). Short-term experiments using seedlings may therefore be more realistic in wetlands than in other systems. However, temperate zone wetlands also have long periods during which adult–adult interactions pre-

dominate. Working with seedlings may well over-emphasise the recruitment phase interactions when competitive effects may be at their lowest, or when they may be different from the adult phase because species have not yet differentiated into widely different sizes and morphologies which typify established wetland vegetation. We also know that juvenile life history tactics may be very different from those of estab-

Table 2 Concordance of competitive effects across either three environments or three species. Effect is measured as the weight of an indicator species (*Carex crinita*, *Gnaphalium uliginosum*, *Lycopus americanus*) grown with neighbour species relative to indicator species grown alone

| Indicator species | Environment | W | χ^2 | d.f. | P |
|-------------------------------------|-------------|------|----------|------|--------|
| <i>Carex</i> (tussock) | tested* | 0.76 | 43.32 | 19 | < 0.01 |
| <i>Gnaphalium</i> (obligate annual) | tested* | 0.60 | 34.20 | 19 | < 0.02 |
| <i>Lycopus</i> (facultative annual) | tested* | 0.49 | 27.93 | 19 | > 0.05 |
| Tested† | control | 0.46 | 26.22 | 19 | > 0.10 |
| Tested† | flooded | 0.43 | 24.51 | 19 | > 0.10 |
| Tested† | infertile | 0.46 | 26.22 | 19 | > 0.10 |

*Competitive effect is tested for concordance across three environments using one indicator species.

†Competitive effect in the specified environment is tested for concordance across three indicator species.

Table 3 Concordance of competitive response across either three environments or three species. Response is measured as the weight of the twenty neighbour species grown with the indicator species relative to neighbour species grown alone

| With indicator species | Environment | <i>W</i> | χ^2 | d.f. | <i>P</i> |
|-------------------------------------|-------------|----------|----------|------|----------|
| <i>Carex</i> (tussock) | tested* | 0.23 | 11.04 | 16 | > 0.80 |
| <i>Gnaphalium</i> (obligate annual) | tested* | 0.42 | 20.16 | 16 | > 0.20 |
| <i>Lycopus</i> (facultative annual) | tested* | 0.29 | 14.05 | 16 | > 0.50 |
| Tested† | control | 0.69 | 31.01 | 15 | < 0.01 |
| Tested† | flooded | 0.60 | 25.20 | 14 | < 0.05 |
| Tested† | infertile | 0.38 | 17.10 | 15 | > 0.30 |

*Competitive response is tested for concordance across three environments using one indicator species.

†Competitive response in the specified environment is tested for concordance across three indicator species.

lished adults (Shipley *et al.* 1989). Here we have a practical constraint in designing such experiments. The need for a large number of similar sized individuals made the use of seedlings unavoidable. In this study we have therefore explored the interactions between species as they pass through the recruitment phase and begin to establish adult morphologies (in the case of perennials). Given the demonstrated

importance of competition among adult wetland plants (Grace & Wetzel 1981; Wilson & Keddy 1986a,b; Gaudet & Keddy 1988; Shipley *et al.* 1989), we suspect that if anything, the experiment would tend to underestimate the effects of competition in general, and tend to underestimate the importance of competitive rankings among adults.

We also cannot know how the competitive rankings of effect and response might have changed through time. For practical reasons, this experiment, like many others (Goldberg & Barton 1992) ran for one growing season and this may have led to underestimates of competitive performance of slower growing species. This could be tested only by comparing rankings across years. Such work is needed. Gaudet (1993) did such a study with adult plants and found results to be correlated across years.

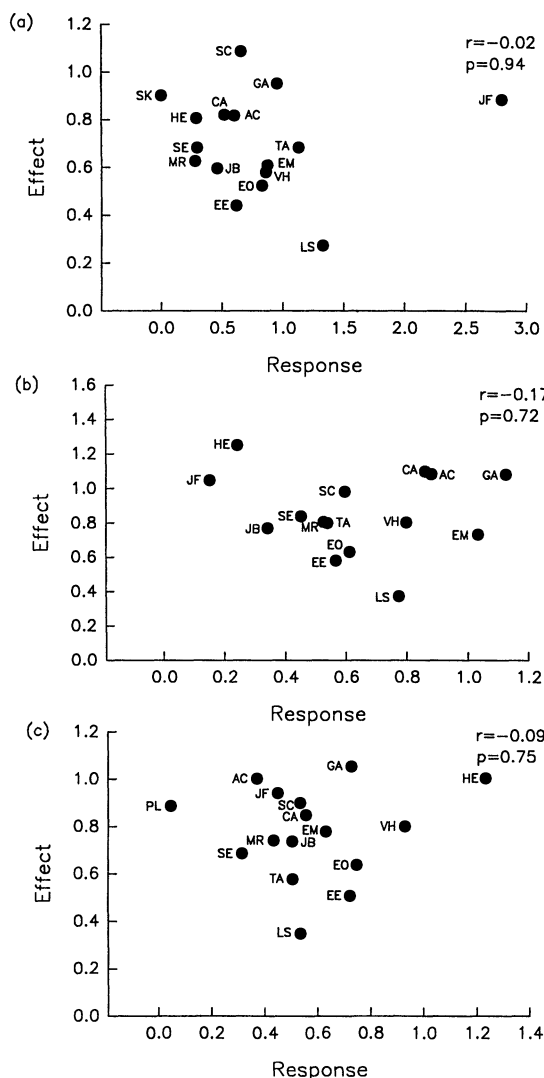


Fig. 5 Correlations between mean relative effect and mean relative response within the (a) control environment (b) flooded environment and (c) infertile environment.

COMPETITIVE EFFECT RANKINGS

In each of the three environments, clear rankings of competitive effect developed after only one growing season. This is consistent with the observation that hierarchies are a general feature of published competition experiments (published studies in Keddy & Shipley 1989; Shipley 1993). This study created two sets of conditions widely known to cause changes in wetland plant communities, namely flooding (e.g. Kozłowski 1984; Spence 1982; van der Valk 1981), and fertility (Wisheu & Keddy 1989; Moore *et al.* 1989). Nevertheless, the resulting rankings were concordant. Other recent work has shown that competitive effect hierarchies are unaffected by soil fertility (Gaudet 1993).

Although some pairs of species showed reversals in competitive performance between environments relative to one another, competitive rankings for the group of species as a whole were correlated among environments. These results emphasize how working with selected pairs of species can prevent the detection of general principles in competition experiments (Keddy 1989), and show that in a broad comparative sense, some plants are inherently better at competition than others. We can therefore begin asking which traits confer competitive ability. By emphasizing simi-

lar kinds of species in competition studies, past workers may have tended to over-emphasise the degree to which the outcome of competitive interactions depends upon minor environmental changes (Keddy 1989; Shipley & Keddy in press).

When the indicator species was changed, the competitive effect rankings changed significantly, in contrast to Gaudet & Keddy (1988) who found nearly identical results using *Lythrum salicaria* and *Penthorum sedoides* in spite of the fact that they belong to different wetland plant guilds (Boutin & Keddy 1993). However, we deliberately chose widely different indicator species to explore the limiting case. Clearly a point is reached when indicator species are so different that the rankings they detect are not concordant. This reinforces the point that traits of plants affect competitive performance strongly. That is, instead of emphasizing the subtle effects of environmental conditions upon competitive interactions, we might seek to link outcomes to the traits of plants themselves.

This result also raises an important methodological issue: which kind of species is the best choice for an indicator species and a target species? More work is needed here. It is probably best to avoid both strong and weak competitors, since this tends to produce many species with similar competitive performances (e.g. Nielsen 1993). A species of intermediate competitive performance may be the best choice as it will produce the best spread of relative competitive performances, enhancing resolution for the next stages of analysis.

If we look for traits linked to relative competitive performance, the strongest plants were species such as *Lythrum salicaria* and *Eleocharis erythropoda*, rhizomatous perennials which occur on relatively fertile high biomass shorelines (Day *et al.* 1988). The weaker ones were *Sabatia kennedyana* and *Gratiola aurea*, which are small partly evergreen perennials which occur on relatively infertile wave washed shorelines (Keddy & Wisheu 1989). Indeed, the latter species are in a group where their effect on the indicator species was not detectable. This is completely consistent with other work on competitive effect which found that larger species were better competitors (Gaudet & Keddy 1988) and that weak competitors were species considered nationally or provincially rare (Gaudet & Keddy 1989). One disturbing feature of these competitive effect patterns is that in all three environments, the invasive exotic *Lythrum salicaria* caused an average reduction of 60% in the yield of neighbours irrespective of habitat. This work suggests that even infertile habitats with rare species are at risk from *Lythrum salicaria*. At the other extreme, the nationally threatened species *Sabatia kennedyana* had consistently the lowest competitive effect; if anything, the data suggest that it has commensal rather than competitive interactions with neighbours. The fact that this commensal effect is most striking in the flooded treatments suggests that neighbours may have

increased soil oxygen levels or reduced water levels through evapotranspiration.

COMPETITIVE RESPONSE RANKINGS

Competitive response (the ability of the 17 neighbour species to tolerate neighbours) showed a different pattern from competitive effect. Response rankings were not concordant across environments when the rankings were based on all three indicator species and there was no concordance across the three environments for any of the species analysed separately. This suggests that competitive response is more sensitive to changes in environment than is competitive effect. That is, the relative ability to reduce the growth of neighbours may be similar across environments and highly dependent on the traits of the species concerned whereas relative ability to tolerate the presence of neighbours is relatively more dependent upon environmental conditions. Apparently the relative ability to tolerate neighbours is a trait which does not vary greatly with the kind of neighbour.

We cannot generalize about species showing strongest competitive responses. *Juncus filiformis* had the strongest response in the control environment, *Gratiola aurea* had the strongest response in the flooded environment and *Hypericum ellipticum* had the strongest response in the infertile environment (Fig. 4). All are typical of sandy infertile shorelines (Keddy & Wisheu 1989). One might be tempted to generalize from this that species of infertile shorelines are more resistant to neighbour effects, but just below them in the response rankings are species such as *Lythrum salicaria* (in the control treatment), *Eupatorium maculatum* (in the flooded treatment) and *Verbena hastata* (in the infertile treatment). These are robust plants with large seed output which tend to germinate in gaps (Boutin & Keddy 1993) and so do not support the above suggestion. Moreover, flooding moves *Juncus filiformis* from being best tolerator of neighbours in the control to being the worst tolerator of neighbours. Similarly, infertility moves *Hypericum ellipticum* from being one of the worst tolerators of neighbours in the control to the best tolerator of neighbours.

EFFECT AND RESPONSE

Competitive effects show different patterns from competitive response. Goldberg & Landa (1991) also found that the mean effect and response were not significantly correlated for either density or biomass although other experiments have revealed different results: a positive relationship was found by Goldberg & Fleetwood (1987) and a negative relationship was found by Miller & Werner (1987). Our results, from the largest data set to date, confirm that one cannot generalize from competitive effect to competitive response. This is surprising given the general import-

ance of competition in the evolution of plants and functioning of plant communities (Grime 1979; Tilman 1982, 1988; Keddy 1989). One would expect them to be correlated. Their apparent independence greatly complicates possible generalizations about competition and competitive performance. The relative importance of effect and response in determining plant species' distributions in nature is not known. Therefore, it is important to determine whether one or the other predominates. If one component is found to predominate in nature then more effort could be focused on that component. This leads to two general questions requiring further attention (1) Are plant species' distributions in the field better predicted from knowledge of competitive effect or competitive response? and (2) Which plant traits are correlated with higher relative competitive effect and higher relative competitive response? Recent work shows that estimates of relative competitive effect are a good predictor of field distribution (Gaudet 1993). As well, plant size and leaf shape are good predictors of competitive effect in both wetland plants (Gaudet & Keddy, 1988) and old field plants (Nielsen 1993). Competitive response is far less studied and understood. Both of the foregoing questions require further attention and will require large studies using many species simultaneously.

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References

- Boutin, C. & Keddy, P.A. (1993) A functional classification of wetland plants. *Journal of Vegetation Science*, **4**, 591–600.
- Campbell, B.D., Grime, J.P., Mackey, J.M.L., Jalili, A. (1992) The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Functional Ecology*, **5**, 241–253.
- Clements, F.E., Weaver, J.E. & Hanson, H.C. (1929) *Plant Competition*. Carnegie Institute of Washington, Washington, DC.
- Day, R.T., Keddy, P.A., McNeil, J. & Carleton, T. (1988) Fertility and disturbance gradients: a summary model of riverine marsh vegetation. *Ecology*, **69** (4), 1044–1054.
- 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*. PhD thesis, University of Ottawa, Ottawa, Ontario.
- Gaudet, C.L. & Keddy, P.A. (1988) Predicting competitive ability from plant traits: a comparative approach. *Nature*, **334**, 242–243.
- Gaudet, C.L. & Keddy, P.A. (1989) Relationship between competitive ability, morphology and field distribution: implications for wetland management. *Wetlands: Inertia or Momentum Proceedings of Federation of Ontario Naturalists*, (eds M. J. B. Bardecki & N. Patterson), pp. 385–390. Federation of Ontario Naturalists, Don Mills.
- Gleason, H.A. (1952) *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada*. Hafner Press, New York.
- Goldberg, D.E. (1990) Components of resource competition in plant communities. *Perspectives on Plant Competition* (eds J. B. Grace & D. Tilman), pp. 27–49. Academic Press Inc., San Diego.
- Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities. A review of field experiments with plants. *American Naturalist*, **122**, 662–696.
- Goldberg, D.E. & Fleetwood, L. (1987) Competitive effect and response in four annual plants. *Journal of Ecology*, **75**, 1131–1143.
- Goldberg, D.E. & Landa, K. (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013–1030.
- Grace, J.B. (1991) A clarification of the debate between Grime and Tilman. *Functional Ecology*, **5**, 583–587.
- Grace, J.B. & Wetzel, R.G. (1981) Habitat partitioning and competitive displacement on cattails (*Typha*): experimental field studies. *American Naturalist*, **118**, 463–474.
- Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.
- Grime, J.P. (1979). *Plant Strategies and Vegetation Processes*, Wiley, Chichester.
- Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- Harper, J.L. 1977. *Population Biology of Plants*. Academic Press, London.
- Keddy, P.A. (1989) *Competition*. Chapman and Hall, London.
- Keddy, P.A. (1990) The use of functional as opposed to phylogenetic systematics: a first step in predictive community ecology. *Biological Approaches and Evolutionary Trends in Plants* (ed. S. Kawano), pp. 387–406. Harcourt Brace Jovanovich, London.
- Keddy, P.A. (1992) A pragmatic approach to functional ecology. *Functional Ecology*, **6**, 621–626.
- Keddy, P.A. & Reznicek, A.A. (1982) The role of seed banks in the persistence of Ontario's Coastal Plain Flora. *American Journal of Botany*, **69** (1), 13–22.
- Keddy, P.A. & Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos*, **54**, 234–241.
- Keddy, P.A. & Wisheu, I.C. (1989) Ecology, biogeography and conservation of coastal plain plants: some general principles from the study of Nova Scotian wetlands. *Rhodora*, **91** (865), 72–94.
- Kozlowski, T.T. (ed.) (1984) *Flooding and Plant Growth*. Academic Press Inc., Orlando, FL.
- Leck, M.A., Parker, V.T. & Simpson, R.L. (eds) (1989) *The Ecology of Soil Seed Banks*. Academic Press Inc., San Diego.
- Miller, T.E. & Werner, P.A. (1987) Competitive effects and responses between plant species on a first-year old-field community. *Ecology*, **68**, 1201–1210.
- 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.
- Nielsen, K (1993) *Predicting competitive ability from plant*

traits: a comparative study of 63 terrestrial herbaceous plant species. MSc thesis, University of Ottawa, Ottawa, Ontario.

- SAS Institute Inc. (1987) *SAS Version 6.04*. SAS Institute Inc., Cary, NC.
- Shipley, B. (1993) A null model for competitive hierarchies in competition matrices. *Ecology*, **74**, 1693–1699.
- Shipley, B. & Keddy, P.A. (in press) Evaluating the evidence for competitive hierarchies in plant communities. *Oikos*, **69**, 340–345.
- Shipley, B., Keddy, P.A., Moore, D.R.J. & Lemky, K. (1989). Regeneration and establishment strategies of emergent macrophytes. *Journal of Ecology*, **77**, 1093–1110.
- Siegel, S. (1956) *Nonparametric Statistics for the Behavioral Sciences*, pp. 213–223. McGraw-Hill, New York.
- Spence, D.H.N. (1982) The zonation of plants in freshwater lakes. *Advances in Ecological Research*, **12**, 37–125.
- Statistical Graphics Corporation (1988) *Statsgraphics Version 3.0*. Statistical Graphics Corporation, STSC Inc., USA.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Tilman, D. (1988) *Plant Strategies and the Structure and Dynamics of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- van der Valk, A.G. (1981) Succession in wetlands: a Gleasonian approach. *Ecology*, **62** (3), 688–696.
- Wedin, D. & Tilman, D. (1991). Dynamics of nitrogen competition between successional grasses. *Ecology*, **72** (3), 1038–1049.
- Wilson, S.D. & Keddy, P.A. (1986a) Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, **67** (5), 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.
- Wisheu, I.C. & Keddy, P.A. (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*. Prentice Hall, Englewood Cliffs, New Jersey.

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