

A comparative approach to examine competitive response of 48 wetland plant species

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Abstract. Competitive ability can be separated into competitive effect (ability to suppress neighbours) and competitive response (ability to tolerate suppressive effect from neighbours), but little is known about the competitive response of plants. A screening trial was conducted in outdoor plant pots where competitive response was measured for 48 wetland species during four months grown with seven established sward species: *Acorus calamus*, *Carex crinita*, *Eleocharis smallii*, *Lythrum salicaria*, *Penthorum sedoides*, *Scirpus acutus* and *Typha angustifolia*. Competitive response was calculated as $100(x_1 - x_2)/x_1$, where x_1 is the weight of the target plant grown alone and x_2 the weight of the target plant grown in the swards. Despite significant differences in biomass and survivorship of the target plants between the sward species, the correspondence, W , of the rank order of the competitive response of target plants grown in the seven sward species was 0.70 ($P < 0.001$). The competitive response values were not significantly correlated with independent measures of competitive effect, relative growth rate or functional classification. Published competitive effect values, however, were significantly positively correlated with RGR. The results suggest a different approach towards the study of competitive response, with a conceptual model including three different response types: (1) escape; (2) foraging; and (3) persistence.

Keywords: Competition; Competitive effect; Relative growth rate; Functional classification; Screening test.

Nomenclature: Gleason & Cronquist (1963).

Introduction

Competition is one of the most important factors controlling species distribution, and it is generally assumed that plant competitive ability varies along natural environmental gradients of fertility (Mueller-Dombois & Ellenberg 1974; Grime 1977, 1979; Tilman 1982, 1985, 1988; Austin 1986; Keddy 1990a, b; Keddy & MacLellan 1991). There has been a good deal of effort to link species' traits with competitive ability for the purpose of predicting species' distribution along fertility gradients. For example, relative growth rate (Grime & Hunt 1975; Shipley & Keddy 1988; Shipley & Peters 1990) and competitive effect (Gaudet & Keddy 1988; Rösch et al.

1997) are important traits related to general plant strategy types and both have been successfully employed to predict herbaceous plant distribution along experimentally controlled (Campbell & Grime 1992), and natural (Gaudet & Keddy 1995) environmental gradients.

Competitive effect, though, is only one aspect of competitive ability. Competitive ability of an individual can be measured in two ways: competitive effect (ability to suppress other individuals) and competitive response (ability to avoid being suppressed) (Jacquard 1968; Goldberg & Werner 1983; Goldberg & Fleetwood 1987; Goldberg & Landa 1991). Both competitive effect and response can be expressed as an empirical ranking in the reduction of some component of individual fitness of a single target species grown with a different neighbour species (Gaudet & Keddy 1988; Goldberg & Landa 1991).

There is a greater understanding of competitive effect than competitive response because more research has been done on competitive effect, at least in terms of multiple species comparisons (Goldberg & Fleetwood 1987; Goldberg & Landa 1991; Keddy et al. 1994; Wilson 1994; Wilson & Tilman 1995). In general, it seems that competitive effect is mainly asymmetric (Connell 1983; Schoener 1983; Keddy 1989; Johansson & Keddy 1991) and produces communities organized in a hierarchical structure (Keddy & Shipley 1989; Shipley 1993; Shipley & Keddy 1994). That is, a small number of plant species are dominants which account for the majority of the biomass, and the remaining subordinate species are numerous and account for relatively little of the biomass. Fast growing, tall plants will often have high competitive effect values (Gaudet & Keddy 1988). Furthermore, the rank order of competitive effect remains relatively constant across habitats varying in productivity (Keddy et al. 1994; Goldberg 1996). Competitive response is less understood, and such studies often lead to ambiguous and conflicting conclusions (Goldberg & Landa 1991; Keddy et al. 1994; Wilson 1994; Gerry & Wilson 1995; also see Goldberg 1996 for a review).

Even the most basic question, whether there is a correlation between competitive effect and response, is unclear. Goldberg & Landa (1991) and Keddy et al. (1994)

found that competitive effect and response were not correlated; while Goldberg & Fleetwood (1987) found a positive relationship, and Miller & Werner (1987) found a negative relationship (but this result may be confounded by population size). Keddy et al. (1994) found that the ranking of competitive response was not concordant across environments varying in productivity, and was insensitive to the species of neighbour; whilst the opposite was true for competitive effect. Wilson (1994) and Gerry & Wilson (1995) showed that the initial size of target plants in an old field consisting of established perennial vegetation did not influence competitive response on either nutrient-rich or nutrient-poor soils. The only apparent consistent pattern has been concordance in the ranking of competitive response among environments with similar productivities, even when the differences in magnitude of response are large (Goldberg 1996). Based on this result, Goldberg has suggested that a hierarchical pattern must exist and that competitive response should be related to specific plant traits (Goldberg 1990, 1996).

Goldberg (1990) has proposed a conceptual model of competitive response, where she first separates the mechanism of competition into effect and response, and then separates the mechanism of competitive response depending on the relative sizes of the competing plants. Small plants that are surrounded by large plants are unlikely to have any appreciable effect on their neighbours. Therefore, Goldberg (1990, 1996) suggested that the ranking of competitive response of the smaller plant will be determined by its ability to tolerate low resources. Alternatively, if target and neighbour are equal in size, Goldberg proposed that the ranking of competitive response would depend on the ability to grow fast and sequester resources quickly.

We used a screening or comparative approach (Grime et al. 1988, 1997; Keddy 1992) for evaluating relative competitive response for as many as 48 species against seven different sward species. The sward species used are all relatively fast-growing, canopy-forming plants. Since the particular mechanism of competitive response is believed to be related to relative sizes of targets and neighbours (Goldberg 1990) we have restricted the sizes. In our design, the size of the targets are much smaller and less mature than their neighbours, which means that they are unlikely to have any significant competitive effect on their neighbours. Furthermore, the target plants are introduced as individuals into a monoculture of mature plants. Therefore, according to Goldberg (1990) the ranking of competitive response of the target plants should be determined by their ability to tolerate depleted resource levels. With this in mind, the following objectives were established:

- Test whether there is a difference in competitive response among the 48 wetland species;
- Test whether the competitive response values of the 48

wetland species varies among seven sward species;

- Determine whether the sward species affect the ranking of response of the target plants ('competitive hierarchies').
- Determine if competitive response is correlated with competitive effect or relative growth rate.
- Test whether the competitive response values for each species can be divided into separate groups according to a functional classification.

Material and Methods

Species

Two sets of wetland species were included in the experiment: sward and target. The sward species were chosen for their tendency to form relatively tall monocultures in wetlands:

<i>Acorus calamus</i>	<i>Carex crinita</i>	<i>Eleocharis smallii</i>
<i>Lythrum salicaria</i>	<i>Penthorum sedoides</i>	<i>Scirpus acutus</i>
<i>Typha angustifolia</i>		

The target species (Table 1) were chosen to represent a broad range of morphology, and life-history types. Representatives of four functional groups (Keddy 1990a; Boutin & Keddy 1993) were included: ruderal, matrix, interstitial, and stress-tolerator. Ruderals are ephemeral plants that flower in their first growing season and have no lateral spreading of their vegetative growth. The matrix and interstitial groups are perennial, fast-growing plants which either spread clonally (matrix), or have a more clumped growth form (interstitial). Stress-tolerators are slow-growing, evergreen rosette species. Often, stress-tolerant wetland plants are also endangered species due to human disturbances and the consequent destruction of their natural habitats (Wisheu & Keddy 1992).

Experimental design

A modified additive completely randomized design was used where individuals of each of the target species were grown with each of the sward species, as well as grown alone ($n = 10$). The total number of pails was 816, with 48 pails in each of 17 rows. The 10 replicates of target species grown alone offer good precision. However, the large number of species used in this experiment prohibited replication of the target plants grown in each of the swards.

Experimental procedure

The experiment was run in a 100-m² outdoor compound at Carleton University, Ottawa, Canada (45° 25' N, 75° 45' W). Over a three-year period from 1988 to 1990 seven wetland species were established in monoculture in 10-liter pails containing a 3:1 ratio of sand to potting soil. Each of the seven sward species was grown once with one of the target species for a total of 336 pails. In the centre

of each pail an empty plastic pot (\varnothing 5 cm) was buried to the rim for the future introduction of a target plant. The initial seeding density of the sward species was ca. 100 seeds per pail. However, each pail was reseeded at the beginning of each growing season in order to obtain a continuous, even sward. Swards were watered and weeded at regular intervals and fertilized each year with 27 g of Nutricoat (14N-14P-14K, a slow-release fertilizer). Over winter, the pails were covered in straw and plastic, as well as being flooded, to minimize frost damage. After three years of growth the swards were well established and of consistent density and height within species.

In May of 1991, 45 wetland species (Table 1a) were collected from various field sites in southern Ontario, Quebec and Nova Scotia. Voucher specimens of each species were stored. Ramets from each species were planted (after removal of the empty plastic pot) into the centre of each of the seven different swards. Three additional annual species, as indicated in Table 1a, were grown from seed and transplanted into the swards. 10 pails with a 3:1 ratio of sand to potting soil were also prepared two years in advance (at the time the swards were established to ensure an equivalent soil environment) for each target species to grow alone for a measure of growth in the absence of competition; i.e. a control. Two measurements were taken on the sward species near the end of the experiment on 10 randomly selected pails from each species: height and available photosynthetic active radiation under the canopy. Light availability (measured as irradiance) was recorded near soil level, in the middle of the sward, using a hand-held LI-COR (model LI-189). SI units were measured in Wm^{-2} . The above-ground biomass of the target plants was harvested at the end of August 1991, oven-dried at 80 °C and weighed.

Analysis

Total above-ground biomass of each of the target species grown in the swards was pooled and compared using *t*-tests against the total above-ground biomass of each of the target species grown alone (dead plants were given a value of zero) to test whether the swards significantly reduced the biomass of the target species.

The differential response of the target plants to each of the sward species was tested using a one-way ANOVA, followed by a Tukey test to separate the treatment means. Data were log-transformed. A Mann-Whitney rank sum test was used to determine whether mortality of the target plants grown alone differed between target plants grown under the swards. Cochran's *Q*-test (Sokal & Rohlf 1981) was used to determine if there was a significant difference in mortality of the target plants between the seven swards.

The height and below-canopy light measurements of the swards were analysed using a one-way ANOVA to determine if there were differences between species. The

mean height and light values for each sward species were correlated with each other and with percent reduction in biomass, and percent survival of the target plants using Pearson's correlation coefficient (Wilkinson 1990).

Two different competitive response values were calculated. The mean competitive response (R_m), which was based on the mean weight of the target species that survived in all seven swards against the mean weight of the target species grown alone, and was calculated as:

$$R_m = 100 (x_1 - x_2) / x_1 \quad (1)$$

where x_1 = weight of the target plant grown alone ($n = 10$); and x_2 = weight of the target plant grown in sward ($n = 7$). The individual competitive response of the target species grown in each of the different swards (R_s) was calculated as R_m but with x_2 now as an individual measure ($n = 1$).

The mean competitive response value was compared with published competitive effect values (Gaudet & Keddy 1988), and published relative growth rate values (Shipley & Peters 1990) (Table 1a). Some experiments concern competitive response vs. effect measured simultaneously (e.g. Goldberg & Fleetwood 1987; Goldberg & Landa 1991; Keddy et al. 1994), but the design of this experiment was not set up to measure competitive effect. It is also, conceivably, a more powerful test to use two wholly independent measures of competitive response and effect in order to test their correlation. For this type of comparison between different published traits it was important that the environmental conditions (i.e. climate, soil, nutrients, grown in pots) were similar for all the tests. ANOVA was also used to determine whether there was a difference between the functional groups of the target species (Boutin & Keddy 1993) (Table 1a) according to their mean competitive response values.

Kendall's test of concordance *W* (Siegel 1956) was applied to determine the degree of agreement in the rank order of the individual competitive response of the target plants grown in the seven swards; *W* varies between 0 and 1, where 1 is complete concordance. Furthermore, the significance of *W* was calculated, where the null hypothesis is no correlation. Therefore, significant concordance does not mean that there are no differences between the seven rankings, only that they are not random with regard to each other (Grace et al. 1993). One cannot run Kendall's test with missing values, and the data set had many missing values ($n = 248$, from a possible $n = 336$) due to plants that did not establish. Therefore, Kendall's test was applied to a very reduced data set ($n = 35$), with only five target species surviving in all of the swards. The two swards with the greatest mortality of target plants (*Carex crinita* and *Scirpus acutus*) were removed, resulting in 18 target plants that survived in all of the remaining five swards ($n = 90$). Kendall's test was applied to this data set as well.

Table 1a. List of the 48 target species included in the experiment. * indicates plants were established as seed, otherwise plants were established as cuttings. The table lists known competitive effect values (Gaudet & Keddy 1988), known relative growth rate values (Shipley & Peters 1990), and the functional classification of the target plants (Boutin & Keddy 1993). - indicates the value has not been determined. **b.** Mean weight of target species grown alone and within the swards, along with *P*-values of Student *t*-tests used to compare the two treatments.

Target species	Competitive effect (%)	Relative growth rate (g/g d ⁻¹)	Functional classification	Mean wt (g) grown alone	Mean wt (g) grown in sward	<i>P</i> -value
<i>Acorus calamus</i>	67	0.17	Matrix ¹	5.686	0.717	0.001
<i>Anemone canadensis</i>	23	-	Matrix ³	0.013	0.017	0.767
<i>Asclepias incarnata</i> ^a	-	0.20	Matrix ¹	17.913	11.447	0.075
<i>Bidens cernua</i> ^{a,b}	91	0.26	Ruderal ¹	23.099	3.277	< 0.001
<i>Calamagrostis canadensis</i>	-	-	Matrix ¹	11.331	3.956	0.019
<i>Carex crinata</i> ^b	58	0.19	Matrix ¹	7.288	0.599	0.005
<i>Carex rostrata</i> ^b	79	0.20	Matrix ³	22.579	6.286	0.007
<i>Cladium mariscoides</i>	-	0.14	Matrix ³	0.594	0.076	0.001
<i>Coreopsis rosea</i> ^b	-	0.26	Matrix ¹	2.812	0.610	0.006
<i>Cyperus rivularis</i>	-	0.25	Ruderal ¹	11.536	0.513	0.015
<i>Dulichium arundinaceum</i>	37	0.19	Matrix ³	1.977	0.429	0.003
<i>Eleocharis acicularis</i>	-	-	Stress-tolerator ²	0.242	0.026	0.014
<i>Eleocharis calva</i>	-	-	Interstitial ¹	14.051	0.834	0.002
<i>Eleocharis smallii</i>	-	0.10	Interstitial ¹	7.494	1.176	0.006
<i>Epilobium ciliatum</i> [*]	-	0.29	Ruderal ¹	3.176	0.747	0.068
<i>Eriocaulon septangulare</i>	25	0.01	Stress-tolerator ²	0.011	0.004	0.114
<i>Eupatorium maculatum</i>	69	0.24	Matrix ¹	7.783	1.176	0.028
<i>Eupatorium perfoliatum</i>	-	0.25	Ruderal ¹	18.628	9.023	0.020
<i>Euthamia galetorum</i> ^b	-	-	Matrix ³	2.498	1.437	0.463
<i>Gnaphalium aurea</i>	-	-	Stress-tolerator ²	0.570	0.061	0.010
<i>Hypericum ellipticum</i>	62	0.35	Interstitial ¹	15.560	7.507	0.221
<i>Iris versicolor</i>	63	0.13	Matrix ¹	5.382	1.061	0.011
<i>Juncus bufonius</i> [*]	-	0.19	Ruderal ¹	3.298	0.003	0.210
<i>Juncus effusus</i> ^a	-	0.27	Interstitial ¹	9.434	2.999	0.026
<i>Juncus filiformis</i>	14	0.18	Interstitial ¹	2.641	0.059	< 0.001
<i>Lophiola aurea</i>	-	-	-	0.478	0.183	0.018
<i>Lobelia dortmanna</i> ^b	4	0.10	Stress-tolerator ²	0.167	0.056	0.074
<i>Lysimachia ciliata</i>	76	0.21	Interstitial ³	1.177	0.141	0.001
<i>Lysimachia thyrsoiflora</i> ^a	77	-	Interstitial ³	4.296	4.007	0.857
<i>Lythrum salicaria</i> ^b	96	0.26	Ruderal ¹	60.299	35.689	0.058
<i>Mimulus ringens</i>	-	0.26	Ruderal ¹	17.933	2.960	< 0.001
<i>Onoclea sensibilis</i>	40	-	Matrix ³	0.442	0.121	0.024
<i>Panicum longifolium</i>	26	0.19	Interstitial ¹	4.029	0.137	0.010
<i>Penthorum sedoides</i>	-	0.30	Interstitial ¹	22.470	4.254	0.002
<i>Phalaris arundinacea</i>	89	-	Matrix ¹	30.863	4.651	< 0.001
<i>Polygonum hydropiperoides</i> ^b	59	-	Matrix ³	1.330	1.219	0.921
<i>Pontederia cordata</i> ^a	-	-	Interstitial ³	4.107	0.996	0.061
<i>Ranunculus reptans</i>	1	-	Stress-tolerator ²	2.438	0.081	0.037
<i>Rumex verticillatus</i> ^b	69	0.20	Interstitial ¹	4.821	4.239	0.750
<i>Sabatia kennedyana</i>	23	0.16	Stress-tolerator ³	0.213	0.057	0.011
<i>Scirpus cyperinus</i> ^b	-	0.19	Interstitial ¹	17.809	3.144	< 0.001
<i>Scirpus fluviatilis</i> ^b	82	-	Matrix ¹	14.714	1.940	< 0.001
<i>Scirpus validus</i> ^b	59	0.20	Matrix ¹	8.742	2.144	0.003
<i>Sparganium eurycarpum</i>	-	0.21	Matrix ³	16.853	2.364	< 0.001
<i>Spartina pectinata</i> ^a	59	0.22	Matrix ¹	29.573	15.801	0.003
<i>Triadenum fraseri</i> ^b	52	0.21	Interstitial ³	0.963	0.365	0.190
<i>Typha glauca</i>	86	-	Matrix ¹	26.736	5.966	0.023
<i>Verbena hastata</i>	-	0.26	Ruderal ¹	2.231	2.874	0.785

¹Boutin & Keddy (1993); ^asurvived in all seven swards; ²Boston & Adams (1986); ^bsurvived in five swards; ³Field observations and unpublished data.

Results

Sward effects on above-ground biomass of target plants

The mean above-ground biomass of the target plant grown in the established swards was generally much less than when grown alone. 33 of the 44 target species experienced a significant reduction in biomass (Table 1b). Only two of the target species, *Anemone canadensis* and *Verbena hastata*, had a greater mean above-ground biomass when grown in the swards, but neither difference was statistically significant. Survival of the target plants was significantly less if grown under the swards (mean 71%) than grown alone (mean 90%) ($T = 3217.5$; $P < 0.001$).

There was a significant difference between the effect of the seven swards on the above-ground biomass of the target species (F -ratio = 14.401; degrees of freedom = 6; $P < 0.001$) (Fig 1a). The survival of the target plants grown in the seven swards was also significantly different (Cochran's $Q = 25.92$, which is greater than the corresponding $\chi^2_{.001[6]}$ which is 22.46 (Fig. 1b). Measurements of both height (F -ratio 70.387; degrees of freedom = 6; $P < 0.001$) and below-canopy light (F -ratio 3.786; degrees of freedom = 6; $P = 0.003$) of the swards significantly varied by species (Table 2). However, neither height nor below-canopy light were significantly correlated with percent reduction in above-ground biomass or percent survival of the target plants (Table 3).

Competitive response

Table 4 gives the mean relative competitive response values of the 48 target species. The rankings of competitive response of the five target plant species that survived in all seven swards had a concordance, W , of 0.70 ($\chi^2_4 = 19.6$; $P < 0.001$) (Table 5). The broader analysis on the rankings of the 18 target plant species that survived in the five selected swards had a concordance, W , of 0.55 ($\chi^2_{17} = 46.75$; $P < 0.001$) (Table 6).

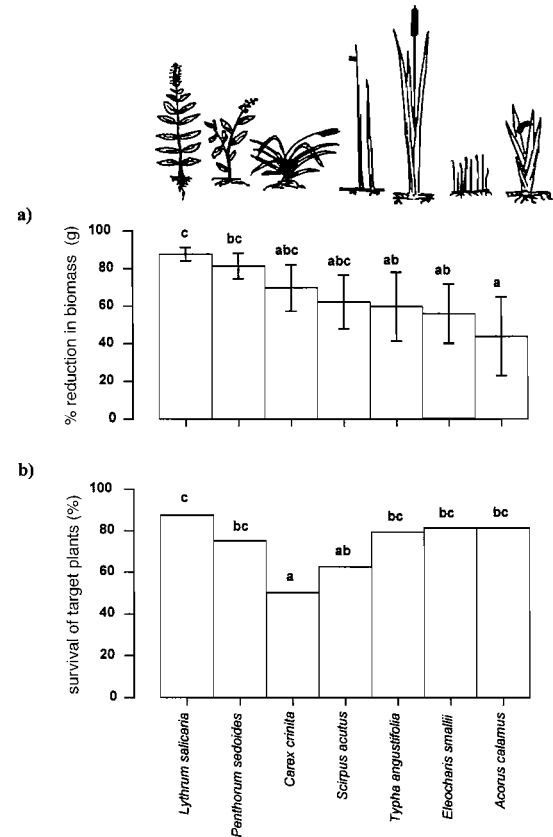


Fig. 1. Effect of sward species on: **a.** the percentage reduction in total above-ground biomass of the target species grown in each sward compared to grown alone; **b.** the percentage survival of target plants. Bars sharing the same letter are not significantly different (Tukey's HSD). Error bars represent 95 % confidence limits.

Table 2. Mean height and below-canopy light measurements of a random subset of 10 of the seven sward species. Values in parentheses are 95 % confidence limits.

Sward species	Height (cm)	Light (w/m ²)
<i>Acorus calamus</i>	105.5 (7.035)	57.276 (22.629)
<i>Carex crinita</i>	87.4 (5.996)	6.932 (4.446)
<i>Eleocharis smallii</i>	81.2 (8.463)	26.248 (14.795)
<i>Lythrum salicaria</i>	112.2 (9.147)	137.132 (91.881)
<i>Penthorum sedoides</i>	59.1 (7.422)	7.541 (3.414)
<i>Scirpus acutus</i>	137.5 (6.025)	98.389 (109.377)
<i>Typha angustifolia</i>	157.8 (15.842)	67.151 (33.512)

Table 3. Correlation coefficients for sward height and below-canopy light measurements, and percentage reduction in biomass and survival of target species. Numbers in parentheses indicate P -value.

	Sward height (cm)	Sward below-canopy light (w/m ²)	Target species reduction in biomass (%)	Target species survival (%)
Sward height (cm)	1.000			
Sward below-canopy light (w/m ²)	0.643 (0.119)	1.000		
Target species reduction in biomass (%)	0.274 (0.552)	0.201 (0.666)	1.000	
Target species survival (%)	0.077 (0.869)	0.417 (0.352)	0.003 (0.995)	1.000

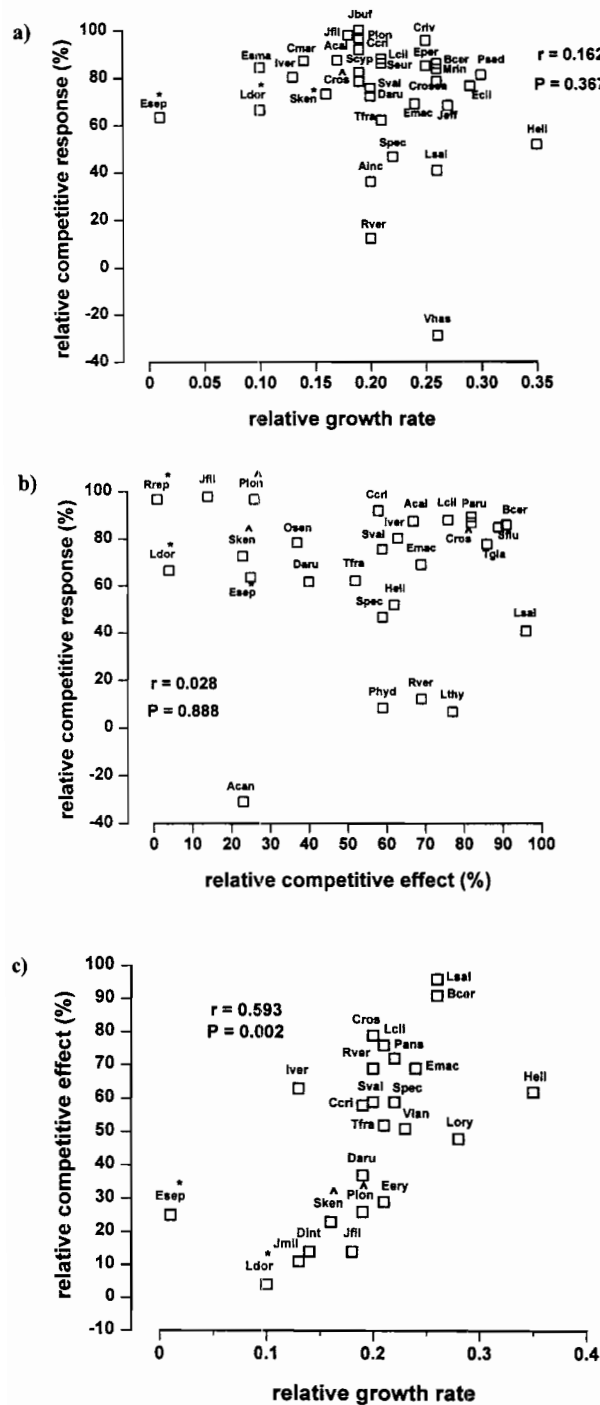


Fig. 2. Correlation between **a.** Relative competitive response and relative competitive effect; **b.** Relative competitive response and relative growth rate; and, **c.** Relative competitive effect and relative growth rate. Relative competitive effect values are from Gaudet & Keddy (1988), while relative growth rate values are from Shipley & Peters (1990). In the figure, * indicates a stress-tolerator and ^ indicates that the plant is nationally rare as well as being a stress-tolerator.

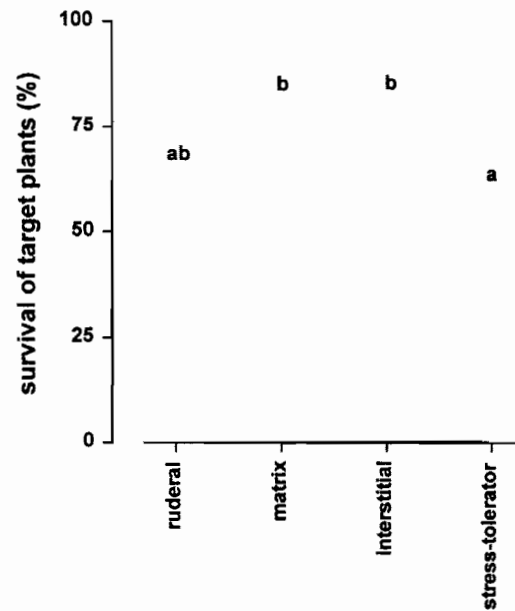


Fig. 3. The relationship between the percent survival of target species grown in the seven swards and the functional classification (Gaudet & Keddy 1993) of the target species. Bars sharing the same letter are not significantly different (Tukey's HSD).

Response vs. effect, rgr, and functional classification

There was no clear relationship between the mean competitive response of the target species (Table 4) and either the published relative competitive effect (Fig. 2a) or relative growth rate values (Fig. 2b). Nor was there a significant difference in competitive response values between the four different functional groups of wetland plants (F -ratio = 0.356; degrees of freedom = 3; $P = 0.785$). Competitive effect values were significantly correlated with relative growth rate (Fig. 2c), as well as being significantly different with respect to the functional group classification (F -ratio = 9.172; degrees of freedom = 3; $P < 0.001$).

The percent survival of the target species varied significantly (F -ratio = 4.976; degrees of freedom = 3; $P = 0.005$); the variation depends on the functional classification (Fig. 3). Matrix and interstitial functional types had significantly greater survivorship than stress-tolerators. It is interesting to note that all five of those target species surviving in the seven swards were fast-growing perennials (matrix or interstitial). Also, 15 of the 18 target species to survive under five swards were fast-growing perennials.

Discussion

Competition in wetlands

Wetlands commonly consist of extensive stands where the biomass is dominated by only a few species (Sculthorpe 1967; Spence 1982; Day et al. 1988; Weiher & Keddy 1995). The success of a juvenile plant to establish in a small gap within a tall canopy will depend to a large extent on its competitive response. The experiment described in this paper included the major genera (*Typha*, *Eleocharis*, *Scirpus*, *Carex*) which account for most of the biomass in temperate wetlands. The results show that all the sward species investigated caused competition resulting in a reduction in above-ground biomass over 50 %, and frequently in the range of 80 % (e.g. *Lythrum salicaria* and *Penthorum sedoides*) when target plants are pooled. It is interesting to note that the two sward species that had the greatest effect on the mean above-ground biomass of the target species (*L. salicaria* and *P. sedoides*) were dicotyledons, while the other sward species were monocotyledons. Differences in competitive ability between monocots and dicots have been observed in other studies (Gaudet & Keddy 1988; Wilson & Tilman 1995; Grime et al. 1997).

Lythrum salicaria is also a problem weed in North America (Weiher & Keddy 1995), and this study further demonstrates its relative ability to reduce the biomass of the native flora. Paradoxically, the survival of the target species grown in *L. salicaria* was the highest. Despite significant differences in both height and below-canopy light between the sward species, there was no correlation with percentage reduction in biomass, or percentage survival, of the target species. A small number of plants were not significantly affected by competition (Table 2) which suggests that plant species vary tremendously in their competitive interactions. The consequent differences in competitive response values among plants will allow us to compare other known important plant characteristics (e.g. competitive effect and functional classification) to determine the variance in competitive response.

There are limitations to this study, which include the artificial growing conditions and the lack of replication of the target species grown under the different sward species. The pros and cons of experimental microcosms for ecological research have been discussed elsewhere (e.g. Carpenter 1996; Fraser & Keddy 1997). We used a screening-type experiment where competitive response values were measured on 48 wetland species. The importance of using large numbers of species for functional interpretations has been emphasized elsewhere (Keddy 1992, 1994; Grime et al. 1997).

Table 4. Mean competitive response values for 48 wetland species in rank order. Competitive response R_m (%) is calculated as $(x_1 - x_2) / x_1 \times 100$, where x_1 = weight of the target plant grown alone and x_2 = weight of the target plant grown in the sward. Lower values indicate that there is little difference in biomass between 'grown alone' and 'grown with neighbours', i.e. a high competitive response value.

Target species	R_m	Target species	R_m
<i>Anemone canadensis</i>	-30.8	<i>Coreopsis rosea</i>	78.3
<i>Verbena hastata</i>	-28.8	<i>Iris versicolor</i>	80.3
<i>Lysimachia thyrsoiflora</i>	6.7	<i>Penthorum sedoides</i>	81.1
<i>Polygonum hydropiperoides</i>	8.3	<i>Scirpus cyperinus</i>	82.3
<i>Rumex verticillatus</i>	12.1	<i>Mimulus ringens</i>	83.5
<i>Asclepias incarnata</i>	36.1	<i>Eleocharis smallii</i>	84.3
<i>Lythrum salicaria</i>	40.8	<i>Phalaris arundinacea</i>	84.9
<i>Euthamia galetorum</i>	42.5	<i>Eupatorium perfoliatum</i>	84.9
<i>Spartina pectinata</i>	46.6	<i>Bidens cernua</i>	85.8
<i>Hypericum ellipticum</i>	51.8	<i>Sparganium eurycarpum</i>	86.0
<i>Lophiola aurea</i>	61.7	<i>Scirpus fluviatilis</i>	86.8
<i>Triadenum fraseri</i>	62.1	<i>Cladium mariscoides</i>	87.2
<i>Calamagrostis canadensis</i>	65.1	<i>Acorus calamus</i>	87.4
<i>Lobelia dortmanna</i>	66.5	<i>Lysimachia ciliata</i>	88.0
<i>Juncus effusus</i>	68.2	<i>Gratiola aurea</i>	89.3
<i>Eupatorium maculatum</i>	69.0	<i>Eleocharis acicularis</i>	89.3
<i>Carex rostrata</i>	72.2	<i>Carex crinita</i>	91.8
<i>Onoclea sensibilis</i>	72.6	<i>Eleocharis calva</i>	94.1
<i>Sabatia kennedyana</i>	73.2	<i>Cyperus rivularis</i>	95.6
<i>Scirpus validus</i>	75.5	<i>Panicum longifolium</i>	96.6
<i>Pontederia cordata</i>	75.7	<i>Ranunculus reptans</i>	96.7
<i>Epilobium ciliatum</i>	76.5	<i>Juncus filiformis</i>	97.8
<i>Typha glauca</i>	77.7	<i>Juncus bufonius</i>	99.9
<i>Dulichium arundinaceum</i>	78.3		

Competitive response ranking

Response rankings were significantly concordant for five target species across the seven different swards, and 18 species across five different swards, despite large differences in the mean above-ground biomass of the target plants grown in each sward type. This significant result suggests that the ranking of competitive response of the target plants is not very sensitive to changes in the neighbouring species despite the magnitude of change due to the relative competitive ability of the neighbouring sward. This is opposite to what was predicted by Goldberg (1990), and asserted by Grubb (1985), but is consistent

Table 5. Ranks assigned to five target plants by seven sward species. See Table 1 for full names of target plants.

Sward species	Target plants				
	<i>Ainc</i>	<i>Lthy</i>	<i>Jeff</i>	<i>Pcor</i>	<i>Spec</i>
<i>Acorus calamus</i>	4	1	5	3	2
<i>Carex crinita</i>	1	2	4	5	3
<i>Eleocharis smallii</i>	2	1	4	5	3
<i>Lythrum salicaria</i>	2	3	4	5	1
<i>Penthorum sedoides</i>	1	2	4	5	3
<i>Scirpus acutus</i>	2	1	4	5	3
<i>Typha angustifolia</i>	2	1	4	5	3

Table 6. Ranks assigned to 18 target plants by five sward species. See Table 1 for full names of target plants.

Sward species	Target plants																	
	<i>Ainc</i>	<i>Bcer</i>	<i>Ccri</i>	<i>Cros</i>	<i>Crosea</i>	<i>Egal</i>	<i>Jeff</i>	<i>Ldor</i>	<i>Lthy</i>	<i>Lsal</i>	<i>Phyd</i>	<i>Pcor</i>	<i>Rver</i>	<i>Scyp</i>	<i>Sflu</i>	<i>Sval</i>	<i>Spec</i>	<i>Tjra</i>
<i>Acorus calamus</i>	12	6	15	14	16	17	13	9	2	7	1	5	3	11	10	8	4	18
<i>Eleocharis smallii</i>	3	12	17	9	15	13	8	7	1	4	14	16	2	11	18	10	6	5
<i>Lythrum salicaria</i>	3	16	14	9	13	12	7	2	6	4	11	17	8	15	10	5	1	18
<i>Penthorum sedoides</i>	1	18	14	11	17	15	9	8	3	4	12	13	2	10	16	7	6	5
<i>Typha angustifolia</i>	8	18	16	7	11	1	12	5	4	6	9	17	2	13	15	14	10	3

with most other studies that have measured competitive response – see Goldberg (1996) for a review. This pattern suggests that there might be plant traits and strategies associated with competitive response (Grime 1977, 1979). However, Keddy et al. (1994) showed that many of the same wetland species tested in the experiment described in this paper do not show concordance in the ranking of competitive response across environments, which implies that there are different mechanisms of competitive response that operate in different environments.

Response vs. effect relationships

There was a large variation in competitive response which could not be explained by relative growth rate measurements or functional group classifications. Furthermore, competitive response was not correlated with independent measurements (Gaudet & Keddy 1988) of competitive effect either, which is in agreement with other studies (Goldberg & Landa 1991; Keddy et al. 1994, but see Johansson & Keddy 1991). On the other hand, competitive effect was significantly correlated with relative growth rate and functional group classifications. Competitive effect is also a good predictor of field distribution (Gaudet & Keddy 1995).

Possible competitive response scenarios

The results from this experiment suggest a different approach towards a conceptual model of competitive response of juvenile plants within an established community. We have devised three possible scenarios of competitive response, which include: (1) the escape response, (2) the foraging response and (3) the persistence response.

The escape response is the rapid upward growth (etiolation) of the apical meristem that occurs under limiting light conditions (Larcher 1995). In this case, upward growth is achieved by stored resources, either in the seed, or stored carbon supplies in a vegetative cutting, and is limited by the relative growth rate of the plant and amount of stored resources. A successful response is when the top of the plant grows above the canopy, in which case the plant will probably flourish. If the top of the canopy is not reached, the escape response will have failed and the

plant is likely to die. Therefore, the escape response is dependent on reaching a critical height. This creates an interesting dichotomy in the competitive response of a plant exhibiting the escape response: boom or bust. We propose that the escape strategy can fall within the functional classification of either a ruderal, matrix or interstitial (Boutin & Keddy 1993). Differences in the success of the escape responders could potentially nullify any differences in competitive response value between the functional classification. It is possible to test each of the competitive response scenarios using comparative screening techniques. A possible test for the escape response would be to first select seeds from a wide range of plant species. Sow the seeds in darkness, or very limited light, and the final height the seedlings achieve (presumably before dying) would give a measure of the critical height of the canopy for each species.

The foraging response is more opportunistic and flexible, and it occurs both above and below-ground (see Campbell & Grime 1989). A plant that employs the foraging response is able to grow quickly towards available resource patches, sequester the resources, and continue the rapid, controlled growth for more available resources. Provided that resources can be found through rapid searching, the competitive response of foragers should be high. In comparison with Grime's CSR model (1977, 1979), the escape and the foraging response could be either a 'ruderal' or a 'competitor' plant strategy type. A possible test for the foraging response would be to first select seeds from a wide range of plant species, and then, sow seeds in darkness (or very limited light). While seedlings grow, patches of light would be made available at varying distances from the main stem. The speed and ability of the plants to respond to the light patches would be a measure of foraging.

Finally, the persistence response is a sit-and-wait strategy. These plants are adapted to living in unproductive habitats and have low relative growth rates (i.e. 'stress-tolerators', sensu Grime 1977, 1979; Boutin & Keddy 1993). Persistence responders store resources. Since they are slow growing, persistence responders are poor at competing for resources compared to a forager. However, persistence responders are able to survive by drawing on stored resources: rate of respiration is greater

than rate of photosynthesis. If conditions do not improve, e.g. a gap in the canopy overhead, eventually persistence responders will die. Generally, though, persistence responders' competitive response values would be quite high because even at the best of times they grow slowly. A possible test for the persistence response would be to select seeds from a wide range of plant species and sow them in darkness (or very limited light). The amount of time to plant death would be the recorded measure of persistence.

Based on this conceptual model, we can make predictions on the plant-response types we are likely to see in environments varying in productivity. The experimental conditions present in this study (high productivity) will accommodate all three competitive response types to varying degrees depending on the duration of the experimental conditions, but mainly the foraging response will be favoured. Some escape responders will have high competitive response values provided they reach the top of the canopy. Others will fail because the critical height of the canopy is too great. The foragers should have relatively high competitive response values. The persistence responders will appear to do well (i.e. they will have relatively high competitive response values), but it would be misleading. In reality, they are drawing on stored resources and would soon die unless competition for available resources was reduced. The survivorship of the functional groups follows these predictions: fast-growing perennials (matrix and interstitial) have the greatest percentage survival, while stress-tolerators have the lowest.

At low productivity we would predict that the most successful response type (and survival) would be persistence. This would explain the lack of concordance across environments found in other studies (see Goldberg 1996). The role of persistence raises the question as to the importance of competitive response at low productivity. Studies have shown that competition both above- and below-ground is minimal at low productivity (Wilson & Keddy 1986a, b; Campbell & Grime 1992; Twolan-Strutt & Keddy 1996). Therefore, it would seem that it is not really a 'competitive' response, but simply the ability to tolerate an environment limiting in resources that would favour persistence. We have demonstrated that canopies significantly reduce growth and survivorship of a wide range of plant species at the juvenile stage, and we propose three different response strategies to competition from canopies.

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