

Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment

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While competition is known to occur among some species in some plant communities, we are not yet able to predict in which environments, or among which species, competitive interactions will be most intense. The objective of this study was to test for competition in a wetland plant community and then to determine which environments and which species were influenced by competition. The study site was the transition zone between shrubs and herbaceous plants on a lakeshore. To test for competitive release, shrubs were removed from treatment plots paired with controls in 25 sections of shoreline and cover of herbaceous species was monitored for 4 years. There were highly significant increases in cover, richness, and diversity in the removal plots, but less than one quarter of the individual species responded significantly. In general, these were small, partly evergreen species with high densities of buried seeds (e.g., *Drosera intermedia*, *Hypericum boreale*). On shores with frequent disturbance and low fertility there was no evidence for competitive release. The reduction in plant cover during a summer with high water levels suggests that lakeshores shift from abiotic to biotic structuring according to the water level in a particular year or series of years. Superimposed upon this is variation attributable to the type of shoreline and the type of species.

Key words: competition, disturbance, exposure, lakeshores, *Myrica gale*, shrubs, wetlands, zonation.

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Si nous savons que la compétition existe entre certaines espèces chez certaines communautés végétales, nous ne sommes pas encore capables de prédire dans quels milieux ni entre quelles espèces, les interactions compétitives seront les plus intenses. Le but de cette étude était de tester pour la compétition dans une communauté végétale des marécages et d'identifier les milieux et les espèces qui ont été influencés par la compétition. Le site d'étude était la zone de transition entre arbustes et herbacées au bord d'un lac. Pour tester pour la remise de compétition, des arbustes ont été enlevés des parcelles expérimentales appariées à des témoins dans 25 sections du littoral et le couvert d'espèces herbacées a été contrôlé pendant 4 ans. Il y a eu des augmentations significatives du couvert, de la richesse et de la diversité dans les parcelles d'enlèvement, mais moins qu'un quart des espèces individuelles ont réagi de façon significative. En général, il s'agissait de petites espèces partiellement à feuilles persistantes et à fortes densités de graines enfouies (e.g., *Drosera intermedia*, *Hypericum boreale*). Sur les rives à perturbations fréquentes et peu fertiles, il n'y a pas eu d'indication de remise de compétition. La réduction dans le couvert végétal au cours d'un été où les niveaux d'eau étaient élevés, indique que les rivages de lacs passent d'une structuration abiotique à biotique dépendant du niveau de l'eau au cours d'une année particulière ou d'une série d'années. Une variation attribuable au type de littoral et au type d'espèces y est superposée.

Mots clés : compétition, perturbation, exposition, bords du lac, *Myrica gale*, arbustes, marécages, zonage.

[Traduit par la revue]

Introduction

We have many studies of plant competition that demonstrate that competition occurs (e.g., reviews by Clements et al. 1929; Harper 1977; Schoener 1983; Connell 1983), but we currently lack the ability to make accurate predictions about where or when competition should be most important (Keddy 1989). This is an important goal for plant ecology. Such predictions could be based upon information about (i) environmental conditions or (ii) the characteristics of the species themselves.

In the first case, we may ask whether, on average, individuals in any particular community experience different intensities of interspecific competition from those in another community. Wilson and Keddy (1986a) and Gurevitch (1986) have shown that the importance of competition changes along natural gradients. In general, there is good evidence that fertile, undisturbed environments are likely to produce intense competitive interactions (Huston 1979; Grime 1973, 1979; Wilson and Keddy 1986a; Thompson 1987; Keddy 1989), although opposing opinions do exist (Newman 1973; Tilman 1987). Field experiments from additional habitats are needed to resolve this matter.

In the second case, the intensity and outcome of competitive interactions might be predicted from species traits (e.g.,

Clements et al. 1929; Grime 1973; Al-Mufti et al. 1977; Goldberg 1982; Menges and Waller 1983; del Moral 1983a, 1983b; Wilson and Keddy 1986b; Gaudet and Keddy 1988). Techniques of comparative ecology (Grime and Hunt 1975; Rorison et al. 1987) may be of particular value here. Gaudet and Keddy (1988) screened 44 plant species for both competitive ability and morphology to test which plant traits were correlated with competitive ability. In general, it appears that large individuals are able to suppress small ones and that differences in size alone may account for a majority of variation in competitive ability.

The objective of this study was to combine a long term field experiment with comparative information on species characteristics to test whether the intensity of interspecific competition varied (i) along a naturally occurring environmental gradient and (ii) among species with different life-history traits.

The experimental system and specific hypotheses

The abrupt transition from woody plants to herbaceous plants occurs on freshwater shorelines throughout the northern temperate zone. This shrub zone may be dominated by a single species such as *Myrica gale*, whereas the herbaceous zone is often diverse (Keddy 1983). Shrubs may control the upper limit of herbaceous species on lakeshores (Keddy 1983; Sharp

and Keddy 1985). The first hypothesis was that competition from shrubs controlled the distribution and abundance of some herbaceous species. Shrubs were therefore removed from 25 treatment plots paired with controls to test whether there was evidence for competitive release in treatment plots. Using field experiments and zoned communities to test for the occurrence of competition is a well-established approach (Sharitz and McCormick 1973; Rabinowitz 1978; Lubchenco 1980; Grace and Wetzel 1981; Goldberg 1982; Wilson and Keddy 1985a; Gurevitch 1986). Because of their size and dense canopies, shrubs may be expected to be competitive dominants (Grime 1979; Keddy 1989) and therefore their removal would be expected to release many smaller species from shading.

Herbaceous plants on shorelines vary greatly in morphology and life history, ranging from small evergreen rosette plants (*Lobelia dortmanna*, *Eriocaulon septangulare*) to large erect plants with deeply buried rhizomes (*Cladium mariscoides*, *Dulichium arundinaceum*). Some of these traits are likely correlated with competitive ability. The second hypothesis was therefore that those species showing evidence of competitive release were different from those that were apparently unaffected by shrubs.

The vertical zonation on lakeshores changes along a second gradient, exposure to waves (Keddy 1983, 1984), and the 25 paired plots represented a range of exposures from an open beach to a sheltered bay. Exposure to waves disturbs plant communities by removing biomass and creates a fertility gradient (Sharp and Keddy 1985; Wilson and Keddy 1985a). The third hypothesis was that the effects of competition would vary along this gradient; the prediction was that competitive release (the difference between treatment and control plots) would decline with increasing exposure.

Methods

The study area (Axe Lake) is located along the boundary of Parry Sound District and Muskoka District east of Georgian Bay in Ontario, Canada (lat. 79°30', long. 45°24'). Its flora and the vegetation zonation have been described in detail elsewhere (Keddy 1981, 1983).

Removing the shrub zone

Twenty-five pairs of quadrats representing shorelines with well-developed shrub cover (primarily *Myrica gale*, with some *Alnus rugosa*) were selected in the following manner on 5 May 1980. Pairs of points were chosen at the extreme lower limit of the shrub zone subject to the following criteria: (i) each pair of points was separated by between 5 and 10 m, (ii) both had visually similar shrub cover, (iii) both had similar substrate (either sand or peat and sand), and (iv) neither differed in any other obvious feature such as seepage or boulders. A peg was then driven in at both points. A coin was then flipped to assign each to a treatment or control randomly. Twenty-five pairs of quadrats were selected to represent a range of exposures from exposed beach to sheltered bay. To estimate shrub biomass, an additional 11 sites were selected. A 0.5 × 0.5 m quadrat with one edge on the edge of the shrub zone was harvested, sorted by species, dried at 100°C, and weighed.

The treatment plots were cleared of shrubs for a 1.5 × 1.5 m area. All woody stems were removed to ground level with pruning shears and 2,4-D (as "Weedone" diluted 1:20 with chainsaw oil) was carefully applied to the cut ends of the stems with small brushes. This was carried out during the 2nd week of May; very little regrowth was present the following August.

Sampling was carried out in late August from 1980 to 1983. All species present in the quadrat were recorded. For each plot, a 0.5 × 0.5 m quadrat was located with one corner touching the marking peg and one side parallel to the waterline. Cover pins were then inserted at 10 cm intervals ($n = 25$) and the number of pins touched was

TABLE 1. Standing crop of shrubs at the very lower limit of shrub zone

Species	Dry wt., $\text{g} \cdot \text{m}^{-2}$ (mean \pm 95% CI)*
<i>M. gale</i>	650.6 \pm 146.8
Other†	65.2 \pm 109.7
Total	715.8 \pm 112.4

* $n = 11$, 0.5 × 0.5 m plots, dried at 100°C.

†Includes *Alnus rugosa* and *Ilex verticillata*.

recorded for each species present. Any regrowth of shrubs in treatment plots was eliminated with pruning shears after sampling.

Wilcoxon's matched-pairs signed-ranks test was the appropriate nonparametric test for this paired design (Siegel 1956). Since effects of competition were the dependent variable of interest, one-tailed tests were used to test for increases in cleared plots relative to controls. Species diversity and evenness were calculated using the Brillouin formula with evenness defined as H/H_{max} (Pielou 1966). When the total cover in a quadrat was zero or only one touch by a pin, the quadrat was excluded from calculations.

Species nomenclature followed Fernald (1950) except for the use of *Triadenum fraseri* for *Hypericum virginicum* and *Xyris difformis* for *X. caroliniana*.

Autecological data was based on information available from studies of the same species and similar vegetation types. The exact sources of each trait are given in the appendix.

Results

Treatment plots had a standing crop near zero since the minimal regrowth was removed each year, whereas control plots had a mean standing crop of shrubs greater than 2500 $\text{g} \cdot \text{m}^{-2}$ (Table 1). Since there were no shrubs at elevations below the sample plots this also illustrates the abruptness of the shrub zonation.

Community responses to shrub removal

Total cover and number of species in a quadrat both increased in treatments (Fig. 1). The data from cover pins showed that diversity increased and that this was due to changes in richness rather than evenness.

Species responses to shrub removal

Measures of frequency showed little response to shrub removal after one growing season (Table 2). After two or more growing seasons, 6 out of 24 species were, at some point, more frequent in the treatment plots: *Eriocaulon septangulare*, *Hypericum boreale*, *Juncus canadensis*, *Rhynchospora fusca*, *Nymphoides cordata*, and *Utricularia cornuta*.

Cover data for the same 24 herbaceous species recorded similar results (Table 3). There were minimal differences after one growing season, with only *Juncus canadensis* increasing significantly in treatments. After two growing seasons, five species showed a significant response (*Drosera intermedia*, *Hypericum boreale*, *Juncus pelocarpus*, *Lycopus uniflorus*, and *Rhynchospora fusca*). Over two more growing seasons *Xyris difformis* also increased significantly in treatments.

In any year less than one quarter of the species showed evidence of competitive release when shrubs were removed (Table 4). Moreover, some species (e.g., *Lycopus uniflorus*) increased significantly in the 2nd year and then declined again to nonsignificance.

The objective of this study was to test for competitive release and therefore one-tailed tests were used. Thus any decrease in cover in treatments would be recorded as nonsignificant. It is

TABLE 2. Comparison of frequency of herbaceous plants in paired control (C) and treatment (T) plots ($n = 25$) in August 1980, 1981, 1982, and 1983

Species	1980			1981			1982			1983		
	C	T	<i>p</i>	C	T	<i>p</i>	C	T	<i>p</i>	C	T	<i>p</i>
<i>Calamagrostis canadensis</i>	4	3	ns	3	5	ns	3	3	ns	1	2	ns
<i>Cladium mariscoides</i>	8	3	ns	9	5	ns	4	5	ns	4	5	ns
<i>Drosera intermedia</i>	20	21	ns	22	21	ns	23	20	ns	16	19	ns
<i>Dulichium arundinaceum</i>	11	11	ns	12	12	ns	9	12	ns	11	10	ns
<i>Eleocharis palustris</i>	8	8	ns	8	7	ns	9	6	ns	6	7	ns
<i>Eriocaulon septangulare</i>	16	19	ns	11	19	0.05	12	20	0.05	15	8	ns
<i>Hypericum boreale</i>	11	14	ns	12	20	0.05	10	21	0.01	13	17	ns
<i>H. ellipticum</i>	10	9	ns	9	10	ns	10	10	ns	8	11	ns
<i>Juncus canadensis</i>	2	10	0.05	3	10	0.05	6	9	ns	2	2	ns
<i>J. filiformis</i>	0	2	ns	0	1	ns	0	1	ns	0	1	ns
<i>J. pelocarpus</i>	18	23	ns	20	25	ns	18	23	ns	16	19	ns
<i>Leersia oryzoides</i>	1	1	ns	2	2	ns	3	2	ns	3	2	ns
<i>Lycopus uniflorus</i>	8	8	ns	8	10	ns	5	6	ns	6	5	ns
<i>Lysimachia terrestris</i>	11	16	ns	19	20	ns	21	19	ns	13	19	ns
<i>Muhlenbergia uniflora</i>	1	1	ns	0	3	ns	0	4	ns	0	4	ns
<i>Nymphoides cordata</i>	8	10	ns	3	11	0.05	11	17	ns	5	10	ns
<i>Rhynchospora fusca</i>	10	11	ns	11	18	ns	11	19	0.05	8	15	ns
<i>Scirpus subterminalis</i>	4	7	ns	8	8	ns	7	12	ns	8	11	ns
<i>S. torreyi</i>	3	3	ns	4	6	ns	4	8	ns	3	8	ns
<i>Triadenum fraseri</i>	8	11	ns	12	13	ns	15	12	ns	16	13	ns
<i>Utricularia cornuta</i>	0	0	ns	3	11	0.05	2	13	0.01	0	12	0.001
<i>Vaccinium macrocarpon</i>	0	0	ns	2	6	ns	3	6	ns	2	5	ns
<i>Viola lanceolata</i>	4	4	ns	7	10	ns	7	12	ns	9	7	ns
<i>Xyris difformis</i>	3	8	ns	5	11	ns	6	10	ns	3	9	ns

NOTE: A χ^2 test corrected for continuity (Siegel 1956) was used to test (one-tailed) whether treatment values were greater than control. Species with frequency < 5 were omitted.

noteworthy, though, that four species showed major declines in cover after shrubs were removed (Table 3): *Calamagrostis canadensis*, *Cladium mariscoides*, *Eleocharis palustris*, and *Hypericum ellipticum*. The first three are robust rhizomatous perennials. These apparent cases of facilitation by shrubs appeared in the 2nd year as well.

Life history traits

Table 5 summarizes the available life-history data for two groups of species: those that at some point increased significantly in clearings and those that did not. In general, those that increased in clearings were small, grew more rapidly, produced smaller seeds, and had higher densities of buried seeds than their counterparts. The appendix provides details for each species.

Variation in space

Treatment effects (competitive release) varied significantly along the exposure gradient over 4 years (Fig. 2). The treatment had least effect on exposed shores and sheltered bays and greatest effects at intermediate levels of exposure.

Discussion

Evidence for competition

Only a small subset of the shoreline species (<25%) showed an increase in frequency or cover when shrubs were removed. Even this relatively low value is an overestimate since rarer species (cover values < 5) were not included in Tables 2 and 3. These results are consistent with Fowler's (1981) study in grassland where significant competitive interactions could be detected for only 14 out of 72 paired interactions of the test species. Similarly, Silander and Antonovics

(1982) found only 8 out of 48 significant interactions in coastal vegetation. In this study, however, all species were tested against one large species comprising a large proportion of the biomass in the community; this makes the small number of significant responses to its removal particularly noteworthy.

The slow colonization of clearings was surprising given at least three methods of propagation: seeds, rhizomes, and plant fragments. The role of seeds was particularly obvious for *D. intermedia*, *H. boreale*, and *L. uniflorus*, where seedlings were frequently observed. Rhizomes from adjacent plants may have invaded treatment plots; *R. fusca* spreads rapidly in this manner. Lastly, fragments of adult plants are dispersed around the lake at high water; pieces of *H. boreale* and *J. pelocarpus* are often stranded by falling water levels.

Although some species were more abundant in clearings, Tables 2 and 3 also show that they still occurred in control plots. This illustrates that species' upper distributional limits do not always occur abruptly at the shrub zone, although there is a significant tendency to do so (Keddy 1983). The individuals found under shrubs (e.g., *Drosera intermedia*, *Hypericum boreale*, *Rhynchospora fusca*) often appeared very different from those in clearings. Under shrubs they were etiolated and showed little evidence of sexual or asexual propagation. Thus, they were washed in from populations beyond the shrubs and persisted, but did not spread. This situation is probably similar to the situation described on sand beaches (Keddy 1982, 1983; Watkinson 1985) where *Cakile edentula* occurs in landward areas only because of a continual rain of propagules. In the absence of this continual immigration, landward populations would be unable to persist. Robust species (e.g., *Calamagrostis canadensis*, *Cladium mariscoides*, and *Dulichium arun-*

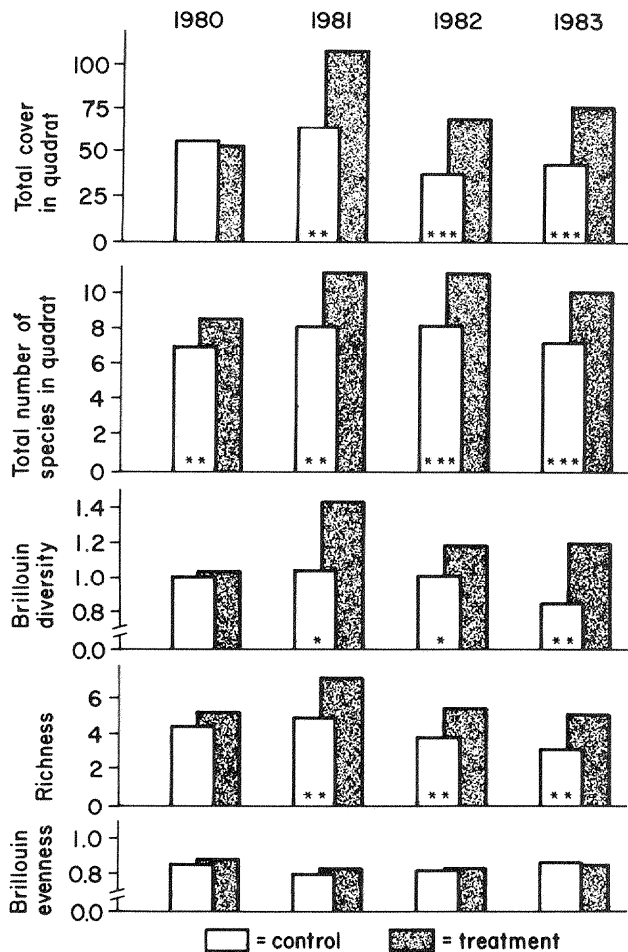


FIG. 1. Changes in plant communities over four growing seasons after the removal of shrubs. Twenty-five pairs of treatment and control plots were compared by one-tailed Wilcoxon's matched-pairs signed-ranks test (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Total cover is cover summed over all species in the plot. Natural logarithms were used to calculate diversity.

dinaceum) were exceptions; they emerged above the shrub canopy and grew vigorously in both control and treatment plots. Interestingly, these were also the species where removal of shrubs caused a decline in cover, suggesting mutualism or commensalism.

Life-history traits

Those species that had distributions that were unaffected by shrubs were in general tall species with small reserves of buried seeds (Table 5). As well, most were capable of vigorous clonal expansion. Given the ability of large species to shade small ones, without themselves being shaded in return, we would expect such species to be, on average, superior competitors; this is consistent with the competitive hierarchy reported by Wilson and Keddy (1986b) and Gaudet and Keddy (1988). This combination of tall leafy shoots and vigorous lateral spread are also traits associated with the ability to suppress other plants (Gaudet and Keddy 1988) and dominate plant communities (Grime 1979). Such species tend to dominate fertile areas with low disturbance (Day et al. 1988).

Those species that significantly increased when shrubs were removed were much shorter. They normally occur on beaches with low biomass, where competition intensity is low (Wilson

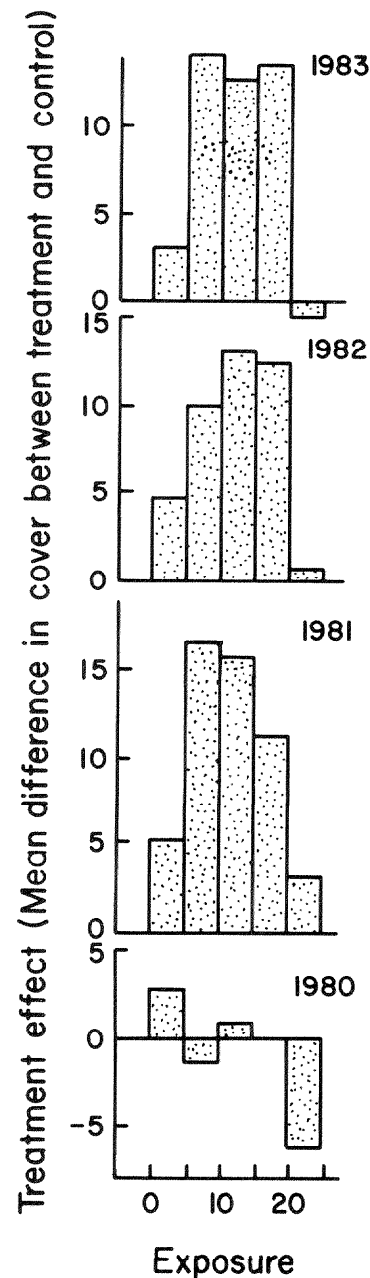


FIG. 2. Treatment effect (difference between control and treatment) for total cover in quadrats, plotted along exposure gradient from sheltered bay (left) to exposed shore (right) and over four growing seasons, 1980–1983. There are no units for the exposure axis since it represents order along the shoreline. Each histogram represents $n = 5$ pairs of treatment and control quadrats combined into one class.

and Keddy 1986a; see also McCreary et al. 1983). These species were also common as buried seeds and had marginally higher growth rates; such traits are consistent with the ruderal strategy (Grime 1979). At the same time, infertile substrates on shorelines disturbed by waves tend to restrict plant growth (Sharp and Keddy 1985; Wilson and Keddy 1985a) and some of these species (e.g., *Juncus pelocarpus*, *Rhynchospora fusca*, *Xyris difformis*, and *Eriocaulon septangulare*) show varying degrees of evergreenness. Boston (1986) and Boston and Adams (1987) have argued that isoetid growth forms are an indicator of the stress-tolerator strategy (*sensu* Grime 1979)

TABLE 3. Comparison of cover of herbaceous plants in paired control (C) and treatment (T) plots ($n = 25$) in August 1980, 1981, 1982, and 1983

Species	1980			1981			1982			1983		
	C	T	<i>p</i>	C	T	<i>p</i>	C	T	<i>p</i>	C	T	<i>p</i>
<i>Calamagrostis canadensis</i>	12	4	—	23	13	—	14	12	—	15	10	—
<i>Cladium mariscoides</i>	33	13	ns	38	27	ns	11	17	—	11	10	—
<i>Drosera intermedia</i>	34	28	ns	22	74	0.005	12	69	0.002	17	72	0.006
<i>Dulichium arundinaceum</i>	17	24	ns	26	44	ns	25	31	ns	25	28	ns
<i>Eleocharis palustris</i>	57	19	ns	60	34	ns	47	30	ns	22	23	ns
<i>Eriocaulon septangulare</i>	17	18	ns	7	7	ns	2	6	ns	1	7	ns
<i>Hypericum boreale</i>	2	3	—	2	24	0.002	1	15	0.020	2	16	ns
<i>H. ellipticum</i>	25	4	ns	7	14	ns	11	17	ns	14	15	ns
<i>Juncus canadensis</i>	4	26	0.016	12	16	ns	9	9	ns	2	3	—
<i>J. filiformis</i>	0	13	—	0	12	—	0	11	—	0	9	—
<i>J. pelocarpus</i>	55	66	ns	80	137	0.045	43	68	0.029	14	39	0.050
<i>Leersia oryzoides</i>	0	1	—	2	10	—	2	1	—	1	2	—
<i>Lycopus uniflorus</i>	9	3	ns	2	13	0.039	5	1	—	7	1	—
<i>Lysimachia terrestris</i>	13	14	ns	20	29	ns	23	20	ns	17	17	ns
<i>Muhlenbergia uniflora</i>	1	1	—	0	6	ns	0	6	—	0	2	—
<i>Nymphoides cordata</i>	0	3	—	2	1	—	2	10	0.031	0	2	—
<i>Rhynchospora fusca</i>	35	33	ns	32	82	0.015	35	81	0.018	25	62	0.021
<i>Scirpus subterminalis</i>	6	13	ns	11	11	ns	2	14	ns	3	9	—
<i>S. torreyi</i>	6	17	ns	5	19	ns	3	9	—	2	10	ns
<i>Triadenum fraseri</i>	20	22	ns	30	48	ns	28	34	ns	33	44	ns
<i>Utricularia cornuta</i>	0	0	—	9	17	ns	0	5	—	0	1	—
<i>Vaccinium macrocarpon</i>	0	0	—	0	11	ns	5	2	—	1	4	—
<i>Viola lanceolata</i>	2	0	—	1	5	ns	4	7	—	6	5	—
<i>Xyris difformis</i>	4	5	ns	5	11	ns	0	14	0.006	0	15	0.008

NOTE: Values in table are total cover recorded out of 625 cover pins (25 quadrats \times 25 pins). Significance (one-tailed) was assessed with Wilcoxon's matched-pairs signed-ranks test, since treatment and control plots were paired. Only species with $n > 5$ in one of the four columns are given. Also recorded were *Aster nemoralis*, *Carex* sp., *Carex lenticularis*, *Eleocharis obtusa*, *Glyceria canadensis*, *Juncus brevicaudatus*, *Potentilla palustris*, *Rhexia virginica*, and *Sparganium* sp. Blanks are given where no test could be done because $n < 3$.

in aquatic plants and specifically mention *J. pelocarpus* and *E. septangulare* as examples.

Spatial variation

Shrubs appear to have little effect on herbaceous plants on exposed shorelines. Frequent disturbance combined with low growth rates may be the predominant factors controlling the distribution and abundance of herbaceous species here. As well, since shrubs occupy only higher elevations on exposed shores (Keddy 1983), the herbaceous species may be reaching their upper tolerance limits.

But what of the results from bays? In spite of low disturbance and fertile substrates, there was little evidence of competitive release. Two hypotheses may account for this and both may be operating simultaneously (Fig. 3). First, there may be insufficient propagules for colonization. In bays, shrubs covered the seasonally flooded zone and abutted the zone of emergent species. There was, therefore, no immediately adjacent source of propagules for those species that occupied the seasonally flooded zone and that responded to the treatments elsewhere (e.g., *Drosera intermedia*, *Hypericum boreale*). This is consistent with the frequency data, which suggested slow dispersal of some species. Second, in bays, shrubs occur at such low elevations that their lower distributional limits may exceed the lower limits of many herbaceous species; thus clearings at the lower limits of shrubs are low on the shoreline and may be too wet for many herbaceous species. Three observations from sheltered bays are consistent with this. First, shrubs do extend lower on the shoreline (Keddy 1983). Second, the floating stems and shrub canopies often

TABLE 4. Summary of release experiment for 24 species: number (proportion) of species showing significant differences between treatment and control over four growing seasons

Source	1980	1981	1982	1983
Cover data	1 (0.04)	5 (0.21)	6 (0.25)	4 (0.16)
Frequency data	1 (0.04)	5 (0.21)	4 (0.16)	1 (0.04)

extend out over the water for a distance of 0.5 m or more, thus covering sites well below their rooting depth. Third, species of the seasonally flooded zone, such as *D. intermedia* and *H. boreale*, were often found only in the highest part of treatment plots, particularly on small peat hummocks, suggesting that most of the plot was too inundated for them to occupy it.

Temporal variation

In years 3 and 4, cover of some species declined in both treatments and controls (Table 3). Similarly, total cover reached a maximum in the 2nd year, declined dramatically in the 3rd year, and increased in the last year (Fig. 1). I suggest this was the result of higher water levels in years 3 and 4. There is no water level monitoring station at the lake, but water levels were approximately 30 cm higher in August 1981 than in August 1980. Record rainfalls in 1981 (Fig. 4) washed out many local roads and produced high water levels that autumn; levels were still atypically high in year 3 (1982). Both treat-

TABLE 5. Comparison of species that increased after shrub removal (*Drosera intermedia*, *Hypericum boreale*, *Juncus pelocarpus*, *Lycopus uniflorus*, *Rhynchospora fusca*, *Xyris difformis*, *Eriocaulon septangulare*) with some selected species that showed no response (*Cladium mariscoides*, *Dulichium arundinaceum*, *Eleocharis palustris*, *Hypericum ellipticum*, *Lysimachia terrestris*, *Triadenum fraseri*)

Characteristic	Increased (n = 7)	No response (n = 6)	p
Mean height (cm)	6.7	27.0	0.002
Total number of buried seeds			
Keddy and Reznicek 1982	44	1	0.001
Nicholson and Keddy 1983	68.9	0.7	0.007
Habitat			
Mean organic content (% less on ignition)	6.4	11.9	0.002
Relative height on shore (cm above July water line)	16.4	20.8	ns
Abundance under shrubs (max. control cover in Table 2)	22.3	27.7	ns
Reproduction			
Weight of 100 seeds (g)	0.012	0.090	0.041
Mean wt. of ramets (g)	0.022	0.326	0.048
Growth rate (g · day ⁻¹)	0.200	0.068	0.048

NOTE: The raw data are given in the appendix; sample sizes were determined by the availability of data for species. Analysis was done with a two-tailed Mann-Whitney *U*-test (Siegel 1956). The latter species were selected because they were the only nonresponding species for which the comparative data was available; note that the first four actually declined after shrubs were removed.

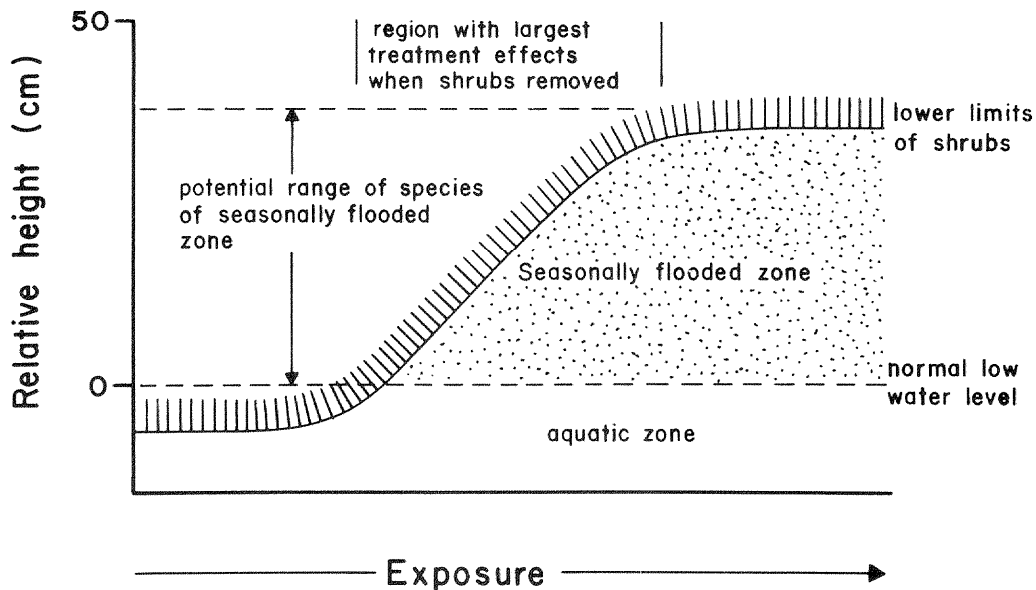


FIG. 3. Conceptual model relating distribution of shrubs and herbaceous species to exposure gradient. The effects of removing shrubs (competitive release) were greatest at an intermediate position along the gradient. The lower occurrence of shrubs in bays (left) may account for the reduced treatment effects in bays. Disturbance and low fertility likely account for reduced treatment effects on exposed shores.

ment and control plots were therefore flooded for a large portion of the growing season.

On lakeshores, the relative importance of competition may vary as water levels change with time. It may be possible to compare the importance of competition with the importance of flooding. Consider total cover as the independent variable of interest (Fig. 1). Each year from 1981 to 1983, treatment values were roughly twice the value of controls. If we take the decline from 1981 to 1982 to be the result of high water levels, we obtain declines of about one third. This first approximation suggests that flooding and shrubs can have roughly equal nega-

tive effects on the growth of herbaceous species. Weins (1977, 1984) has convincingly argued that critical structuring agents may operate for only short periods of time; this is one reason why MacArthur (1972) argued that examination of indirect evidence may be the best way to test for the importance of competition in natural communities.

Water levels fluctuate within and among years to varying degrees in all lakes. Some shoreline floras appear to persist only by exploiting temporary periods of low water (Keddy and Reznicek 1982). Lakeshores, therefore, may be typical of many natural systems, in that communities oscillate between

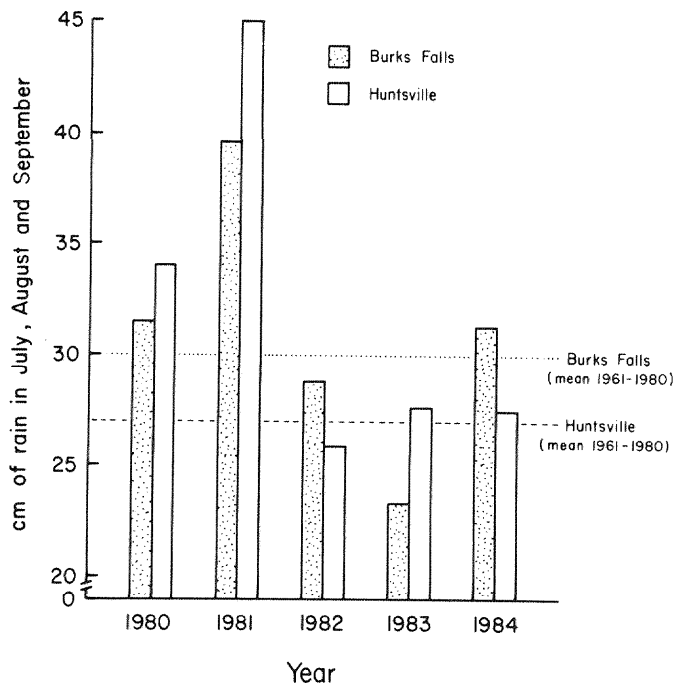


FIG. 4. Accumulated rainfall over the duration of the field experiment compared with means for the preceding 20 years. Burks Falls and Huntsville are the two nearest stations with precipitation data. The extremely high rainfall in the summer of 1981 produced exceptionally high water levels in Axe Lake in autumn 1981 and much of 1982.

years where structuring is imposed by biological forces such as competition (e.g., 1981) and other years where structuring is imposed by abiotic factors such as flooding (e.g., 1982). Only long-term experiments will be capable of detecting this year to year variation.

Community responses to shrub removal

One might conclude that shrubs have relatively little effect on herbaceous shoreline plants. The cumulative effect of small changes, however, produced highly significant differences in community level attributes (Fig. 1). The removal of shrubs produced more diverse herbaceous plant communities, with an extra three species in each 0.5×0.5 m² plot. The species by species analyses show that this was the result of invasion by small species such as *Hypericum boreale*, *Drosera intermedia*, and *Xyris difformis*. Cover was also greater once shrubs were removed. Individual pairwise interactions may therefore seriously underestimate the effect that shrubs have upon community composition, which is one reason why measures of diffuse competition (Wilson and Keddy 1986a) combined with dependent variables summarizing community attributes (Keddy 1987) may be a particularly useful way of exploring competition in plant communities.

Competition and zonation

There is growing evidence that competition controls the distributional limits of vascular plant species found along environmental gradients such as soil pH (Grime 1963), soil depth (Sharitz and McCormick 1973), soil moisture (Gurevitch 1986), water depth (Grace and Wetzel 1981), soil fertility (Goldberg 1982), and salinity (Snow and Vince 1984). This study shows that competition also affects plant zonation on lakeshores, but that the details of the situation will vary with

the species, environment, and year that is selected. A general model for zonation based upon competitive hierarchies is presented in Keddy (1989).

The above studies are consistent with work from the rocky intertidal zone (e.g., Connell 1972; Lubchenco 1980) where there is a fundamental asymmetry in the way in which competition acts upon species' distributions: competition may control one distributional limit and abiotic factors the other. It may be a general principle for most zoned communities that one end of the gradient is preferred by most species and interspecific competition then determines the ability of species to extend into this preferred zone. The species least able to tolerate intense competition in the preferred zone would be stress tolerators or ruderals (*sensu* Grime 1979). On lakeshores, many species appear to be stress tolerators that possess a variety of morphological and physiological adaptations to allow them to tolerate flooding (e.g., Sculthorpe 1967; McManmon and Crawford 1971; Barclay and Crawford 1982; Hendry and Brocklebank 1985). Some might actually grow better further landward in the shrub zone, but may be prevented from occupying this zone by the shrubs. Shallow water species such as *Eriocaulon septangulare* may be competitive subordinates and stress tolerators rather than being specialized to occupy only shallow water environments.

Conclusion

On lakeshores, shrubs would appear to be competitive dominants, with tall shoots, dense canopies, and vigorous clonal growth. Yet only a small subset of the flora increased when shrubs were removed. The greatest evidence for competitive release was detected in small species that normally occupy sandy, seasonally flooded shorelines. When comparing environments, competitive release was lowest in sites with low fertility and high disturbance. Competition appeared less important for large species, on regularly disturbed sandy shores, and during high water periods.

Recent reviews have discussed the need to determine how the effects of competition vary with space and time and among taxa (e.g., Tilman 1982; Schoener 1983; Connell 1983; Weins 1984). This study illustrates four approaches likely to be generally applicable. (i) By evaluating a large number of species simultaneously, it is possible to determine the proportion of the species with significant competitive release. In this case, less than 25% of species exhibited competitive release. One may either evaluate pairwise interactions (e.g., Fowler 1981; Silander and Antonovics 1982) or choose a probable dominant and measure the response of all other species to its removal. (ii) By choosing a community with a wide range of life histories, it may be possible to find different groups of species with different sensitivities to competition. In this case, the distribution of small ruderal species appeared to be most restricted by the zone of shrubs, whereas large, leafy, rhizomatous species were less affected. (iii) By using naturally occurring environmental gradients it is possible to examine whether the intensity of competition varies spatially. (iv) Maintaining the experiment for several consecutive years provides an assessment of temporal variation in competitive effects. In this case, the abundance of shoreline species and effects of competition changed significantly as water levels changed. Peters (1980) has emphasized the importance of prediction in ecology. These data from lakeshores illustrate that it may be possible to predict in which habitats, and with which species, competition is a significant structuring agent.

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Appendix

Comparison of ecological traits of species responding and not responding to the removal of shrubs

Characteristic	Increased after treatments						
	<i>Drosera intermedia</i>	<i>Hypericum boreale</i>	<i>Juncus pelocarpus</i>	<i>Lycopus uniflorus</i>	<i>Rhynchospora fusca</i>	<i>Xyris difformis</i>	<i>Eriocaulon septangulare</i>
Abundance as buried seeds ^a							
Keddy and Reznicek 1982	44	6	19	1	7	10	221
Nicholson and Keddy 1983	85	5	21	0	173	0	198
Habitat							
Mean organic content ^b	11.08	3.83	6.31	8.72	5.91	6.93	2.17
Relative height on shore ^c	17.5	17.5	17.5	32.5	27.5	20	-17.5
Abundance under shrubs ^d	34	2	55	9	35	4	17
Reproduction							
Wt. of 100 seeds ^e	0.0012	0.0006	—	0.0165	0.0431	0.0018	0.0094
Mean wt. of ramets ^f	0.017	—	0.005	—	0.026	0.022	0.038
Growth rate ^g	0.12	—	0.53	—	0.18	0.13	0.044
Mean height (cm) ^h	2.3	6.8	8.2	6.3	18.2	3.8	1.2
Characteristic	No significant increase						
	<i>Cladium mariscoides</i>	<i>Dulichium arundinaceum</i>	<i>Eleocharis palustris</i>	<i>Hypericum ellipticum</i>	<i>Lysimachia terrestris</i>	<i>Triadenum fraseri</i>	<i>p</i> ⁱ
Abundance as buried seeds ^a							
Keddy and Reznicek 1982	5	0	0	0	0	1	0.001
Nicholson and Keddy 1983	3	1	0	0	0	0	0.007
Habitat							
Mean organic content ^b	11.86	14.11	8.78	10.47	12.11	14.18	0.002
Relative height on shore ^c	17.5	12.5	5	32.5	27.5	30	ns
Abundance under shrubs ^d	33	17	57	25	14	20	ns
Reproduction							
Wt. of 100 seeds ^e	0.3078	0.0864	0.0428	0.0029	—	0.0094	0.041
Mean wt. of ramets ^f	0.829	0.316	—	0.014	0.423	0.050	0.048
Growth rate ^g	0.026	0.051	—	0.12	0.050	0.095	0.048
Mean height (cm) ^h	45.2	33.8	33.3	9.3	29.7	10.5	0.002

^aData from Matchedash Lake, a floristically similar lake 65 km south of Axe Lake. Figures are total number of seedlings germinated from sediment samples (Keddy and Reznicek 1982). In Nicholson and Keddy (1983), 111 *Hypericum* seedlings could not be assigned to species; I conservatively assume 5% of these were *H. boreale*.

^bSample units $n = 243$ were collected from Axe Lake. Organic content was measured as loss on ignition at 400°C. Data from Wilson and Keddy (1985b).

^cHeight in cm above July waterline; maxima from frequency in $n = 25$ transects collected as described in Keddy (1983).

^dMaximum cover observed on controls in 1980 (Table 2).

^eUnpublished data from D. Moore. Seeds were dried at 60°C for 24 h prior to weighing.

^fRamets collected in May 1983 and dried at 60°C for 24 h.

^gMaximum observed over the range of substrates provided in Wilson and Keddy (1985b). Growth rate measured as $\text{g} \cdot \text{day}^{-1}$.

^hHeight of typical ramets ($n = 10$) of each species measured at Axe Lake in August 1985 by S. Wilson.

ⁱComparison of all species using two-tailed Mann-Whitney *U*-test (Siegel 1956).