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Coexistence and interference in two submersed freshwater perennial plants

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Summary. Interactions between two codominant submersed freshwater perennial plants, *Eleocharis acicularis* (L.) R. and S. and *Juncus pelocarpus* forma *submersus* Fassett, were studied in a softwater lake. Analysis of segregation indicated a nonrandom arrangement of individual rosettes of each species with respect to rosettes of the other species. Factors influencing growth of the species were examined using de Wit replacement series replicated four times at five ratios, under three environmental treatments: *Sphagnum* peat, double field density, and shading, and a control.

Plants grown in pure culture showed no significant difference in yield between the two species. When plants were grown in mixture, there were significant differences between species. Yields of both species were significantly different among environmental treatments. A significant effect of *Eleocharis*:*Juncus* ratio in the double density treatment resulted from interference among conspecific neighbors. Relative Yield Totals ranged from 0.84 to 1.0 for all four treatments, and ratio diagrams indicate stable coexistence through the growing season under all four environmental regimes. Interspecific interference was less important than environmental factors and intraspecific interference in determining growth in these experiments.

Eleocharis and *Juncus* are nonrandomly intermingled, and can coexist under a variety of environmental manipulations. This outcome is consistent with their reported distributions in nature. The mechanism that permits this stable coexistence awaits explanation.

Introduction

Competitive interactions are commonly assumed to control community structure (e.g. May 1981). However, direct demonstrations of competition in natural communities (e.g. Werner 1978; Werner and Hall 1976; Grace and Wetzel 1981; Silander and Antonovics 1982) are surprisingly few. Nonrandom patterns in vegetation may reflect environmental patterns, demographic processes, or interspecific competition (Pielou 1977). Laboratory manipulations of populations can detect competition, but results may be artifacts of experimental design, and in any case demonstrate only the possibility, but not the magnitude or importance, of competition in nature (McIntosh 1970). Clear identification and demonstration of pattern induced by competition in communities will most likely come from experimental studies of groups of species that appear likely to compete on

the basis of morphological similarity or similar ecological affinity.

The lacustrine littoral zone community offers several advantages for competition studies. Submersed communities of oligotrophic lakes are characterized by morphologically similar rosette plants (Swindale and Curtis 1957). These species are commonly segregated in depth zones (Hutchinson 1975); however, the depth ranges of the species show considerable overlap (Swindale and Curtis 1957; Moeller 1975). Overlap and number of species are greatest in shallow waters (less than 2–3 m depth) with high light intensity (Moeller 1975; Johnsen 1978). *Eleocharis acicularis* (L.) R. and S. (Cyperaceae) and *Juncus pelocarpus* forma *submersus* Fassett (Juncaceae) commonly co-occur in shallow water of North American oligotrophic lakes (Moeller 1975; Johnsen 1978; Swindale and Curtis 1957). They are remarkably similar in appearance; Johnsen (1978) found the species to be so intimately associated in dense mats that she did not attempt to distinguish them in the field. Both species (hereafter referred to by their generic names) produce rosettes along a creeping rootstock (Muenscher 1944). *Eleocharis* grows in tufts of leafless erect stems 5–15 cm high, uniformly 0.25–0.5 mm thick (Gleason and Cronquist 1963). *Juncus* bears erect green leaves, 5–10 cm high (Muenscher 1944) with clasping bases. The leaves are flattened and tapering, with incomplete cross markings (Fassett 1957). With practice, they can be reliably distinguished in the field. Because of their striking morphological similarity and close association in littoral communities, we undertook an empirical and experimental investigation of interactions between these species.

Neighbor relations of rosettes in the field were analyzed using transects through naturally occurring stands of *Juncus* and *Eleocharis*. Competition experiments were designed to mimic natural conditions as closely as possible by planting replicated de Wit replacement series (de Wit et al. 1966) at natural density in pots in a lake. Additional de Wit series were planted under modified environmental conditions *in situ*. A shading treatment examined responses under low light levels, simulating conditions of increased turbidity that could result from eutrophication. A series at twice the mean field density allowed us to examine competitive effects for density dependent responses. A fourth de Wit series was planted in *Sphagnum* peat instead of lake sediment, to assess effects of *Sphagnum* on the competitive interaction of the two species. *Sphagnum* is common on lake margins in northern Wisconsin and upper Michigan, USA, and is reported to be common in lakes subjected to acid precipitation (Grahn 1977).

Materials and methods

Roach Lake is a relatively clear, acid lake (Secchi disk transparency = 3.7 m, pH = 5.1) located on the University of Notre Dame Environmental Research Center in Gogebic Co. MI (Sect. 10 of T44N R42W) and Vilas Co. WI (Sect. 7 of T43N R8E). The submersed macrophyte community consists of the following rosulate perennials in addition to *Eleocharis* and *Juncus*: *Myriophyllum tenellum* Bigel., *Lobelia dortmanna* L., *Gratiola lutea* forma *pusilla* (Fassett) Pennell, *Eriocaulon septangulare* With., *Pontederia cordata* forma *taenia* Fassett, and *Isoetes braunii* Dur., plus the annual *Elatine minima* (Nutt.) Fisch. and Meyer (nomenclature follows Fassett 1957). The study site was located on the NW shore of a small bay, between the 1.0 and 1.5 m depth contours. Criteria for site selection included depth contour, accessibility, suitability for *Juncus* and *Eleocharis*, and protection from disturbance.

To determine the spatial relationships of *Juncus* and *Eleocharis*, two transects were run along the 1.5 m depth contour in August 1982, when the plants were near maximum seasonal biomass. Rosettes were recorded in order along the transects, and presence or absence of each species was noted in 5 cm segments. Pielou's (1962) analysis of segregation was used to test the null hypothesis that the two species are randomly arranged with respect to one another. The scale of pattern for each species was analyzed using the random pairing technique (Ludwig and Goodall 1978).

Each de Wit replacement series (de Wit 1960) used five initial ratios of individual rosettes of the two species (20:0, 15:5, 10:10, 5:15, and 0:20). A complete replacement series was established for each of the four treatments: a control near mean field density (0.8 plants/cm²), a double density treatment (1.6 plants/cm²), a treatment with plants rooted in *Sphagnum* peat instead of lake sediment, and a shading treatment. In the shading treatment pots were placed under a fiberglass-mesh window screen, suspended on a galvanized iron frame. The screen decreased available photosynthetically active radiation by 47%. Every combination of treatment and ratio was replicated four times, with replicates arranged in a randomized block design to account for effects of depth.

Individuals of *Juncus* and *Eleocharis* were collected by snorkelers, and healthy, average-sized rosettes were selected in the laboratory. Following a standard 3 shakes to remove excess water, the initial fresh weight of plants of each species was determined for each pot. A 5 cm × 5 cm grid was constructed and 20 plants were randomly allocated to grid positions. For the double density treatment, 40 plants were randomly placed in each pot. Sediment and sand from Roach Lake were obtained with an Ekman dredge. *Sphagnum* peat was gathered from a nearby bog. Plastic pots (12.5 cm diameter × 9 cm deep) were filled with 5 cm of coarse gravel, 3 cm of sediment, and covered with about 1 cm of sand to stabilize the plantings. Pots for each treatment were assembled in laboratory aquaria, immediately transported in water to the lake, and placed at the study site by SCUBA divers. The experiment lasted from 4 June to 15 August 1981, approximately 70% of the duration of summer stratification in Roach Lake.

All pots were harvested after 66 to 72 days. Plants of each species from each pot were separated, placed in labelled packets, oven-dried (70° C, 24 h), and weighed. The

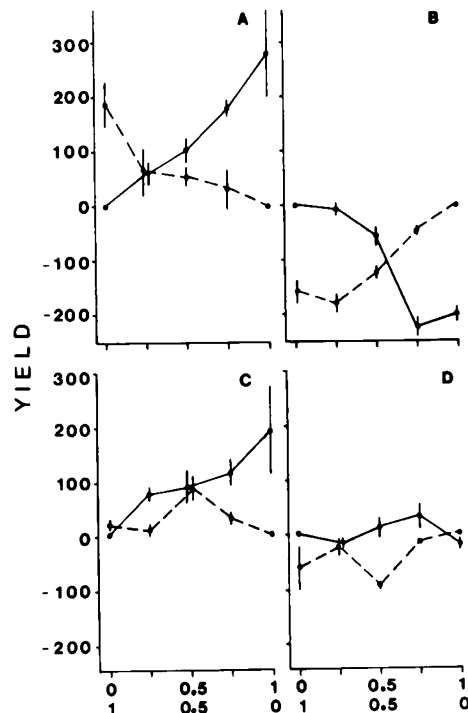


Fig. 1 A–D. Yield in mg growth per pot per species versus ratio in each environmental treatment. Each point represents a mean of 3 or 4 replicates with standard errors indicated. Solid lines indicate *Eleocharis* and broken lines indicate *Juncus*. A = Control, B = Double density, C = *Sphagnum* peat, D = Shading

fresh weight to dry weight ratio was determined from a sample of 50 field-collected plants of each species. Initial fresh weights of experimental plants were divided by this ratio to estimate initial dry weight.

Results

Similar spatial patterns occurred in the two transects. Mean run lengths were 3 rosettes for *Eleocharis* and 3 to 4 rosettes for *Juncus*. Analysis of run length distributions by the method of Pielou (1962) showed that the species were significantly segregated ($P < 0.0001$ for the null hypothesis that the species are arranged randomly with respect to each other). Patch sizes estimated by the random pairing method (Ludwig and Goodall 1974) were 20 cm–30 cm for each species.

Standard de Wit diagrams (Fig. 1) show average growth per pot of each species in each treatment as a function of ratio. Shading, density, and sediment type had highly significant effects on yield in pure culture ($F_{3,23} = 9.60$, $P = 0.0003$). The species' yields when grown alone were not significantly different from one another ($F_{1,23} = 0.71$, $P = 0.41$), indicating that in pure culture they responded similarly to the environmental treatments. *Eleocharis* and *Juncus* both showed high yields in the control treatment, and low yield under double density conditions. Both species responded negatively to increased proportions of conspecifics in the double density treatment. In the peat moss treatment, *Eleocharis* showed vigorous rhizome development, and achieved a higher yield. In the shading treatment, both species had low yields, but not as low as in the density treatment. Negative responses to conspecifics did not occur in the shading treatment.

Table 1. Three-way analysis of variance. Response variable is yield in $\ln g \text{ dry wt} \cdot \text{day}^{-1}$. SP is the species effect, RAT is the ratio effect, and TRT is the effect of environmental treatments

Source	DF	Mean Square	F value	Pr > F
SP	1	0.00001429	7.05	0.0104
RAT	3	0.00000108	0.53	0.6655
TRT	3	0.0000823	40.58	0.0001
SP*RAT	3	0.00000022	0.11	0.9495
SP*TRT	3	0.00000158	0.78	0.5107
RAT*TRT	9	0.00000738	3.64	0.0007
SP*RAT*TRT	9	0.00000145	0.72	0.6945
ERROR	93	0.00000203	—	—

To test for ratio effects, all experimental results were combined in a 2 species \times 5 ratios \times 4 environmental treatments analysis of variance. Final yield was adjusted for the duration of each environmental treatment by the transformation: $\text{Yield} = \ln(1 + (\text{DWF}/\text{DWI}))/t$, where DWF and DWI are final and initial dry mass per species per pot, respectively, and t is the growth period in days. Approximate normality of residuals was confirmed by normal probability plots (Sokal and Rohlf 1981).

Both species and environmental treatments showed significant differences in yield (Table 1). The interaction between ratio and treatment was significant because negative responses to conspecifics occurred in one treatment (double density), while positive responses to conspecifics occurred in other treatments. Effects of ratio were weak and not significant.

Harper (1977) suggests the use of Relative Yield Totals as a measure of interference between species. The Relative Yield of a species I is calculated as $\text{RYI} = (\text{yield of species } I \text{ in mixture})/(\text{yield of species } I \text{ in pure stand})$. By calculating the RY for each species in a particular mixture and summing the two, a Relative Yield Total (RYT) is obtained which describes the kinds of demands the two species may be making on some limiting resource. Values of $\text{RYT} = 1.0$ imply the species are responding independently and similarly to their environment. $\text{RYT} > 1.0$ results from mutual enhancement of their growth, as might result from, for example, enhanced efficiency of resource use when growing together. Values of $\text{RYT} < 1.0$ indicate mutual depression, the result of mutual interference.

Relative Yield Totals averaged across the four treatments ranged from 0.84 (S.D. = 0.29) to 1.0 (S.D. = 0.4). Average RYT for each of the four treatments overlapped considerably at each mixture ratio, and there was little segregation into discrete treatment values. In all treatments, RYT was approximately equal to one at all ratios.

Plots of yield of the two species on perpendicular axes (Fig. 2) provide a convenient means of assessing mutual enhancement or antagonism. If the species are not interacting ($\text{RYT} = 1.0$), then yields in mixtures will tend to lie along the line connecting the points (1,0) and (0,1) (Harper 1977). To assess the degree of deviation from $\text{RYT} = 1.0$, we tested the null hypothesis that the average distance of points (representing pots containing mixtures of the two species) from the reference line equalled zero. Distances were determined along the perpendicular from each point to the reference line, and compared to zero using Student's t -test. We failed to reject the null hypothesis for all treatments (control, $t = 0.975$, $df = 11$, $P > 0.38$; density, $t =$

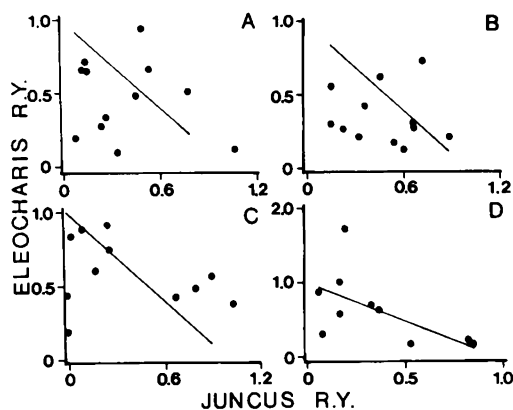


Fig. 2A–D. Relative Yield Totals for each environmental treatment. Each point represents a single pot. A = Control, B = *Sphagnum* peat, C = Double density, D = Shading

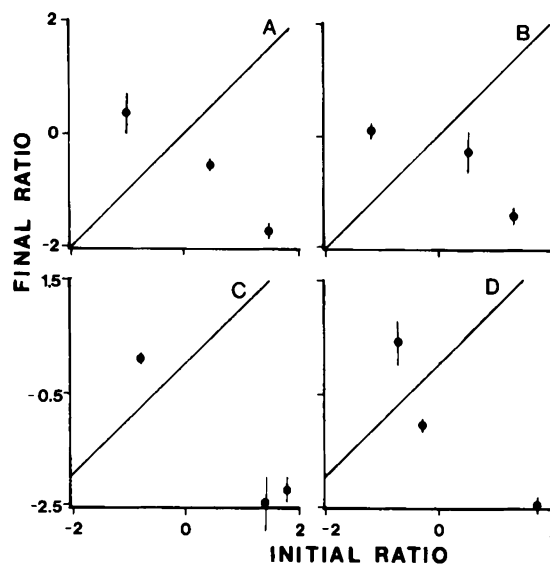


Fig. 3A–D. Plots of \ln initial weight ratio of *Eleocharis:Juncus* versus \ln final weight ratio. Each point represents the mean of 3 or 4 replicates at each of the three mixture ratios, for each environmental treatment, with standard errors indicated if larger than the data point. A = Control, B = *Sphagnum* peat, C = Double density, D = Shading

0.301, $df = 10$, $P > 0.772$; peat, $t = 1.95$, $df = 11$, $P > 0.081$; shading, $t = 0.025$, $df = 9$, $P > 0.943$).

Plots of the ratio of final yield against the initial ratio have been used to reveal frequency-dependent interactions and to predict the outcome of competition during the growing season (de Wit 1960). If all final ratios lie above or below a line of 45° , one of the species will drive the other to extinction. If the plot has a slope < 1 , a stable equilibrium with coexistence of the two species is indicated. A slope > 1 indicates an unstable equilibrium, with outcome dependent on the initial ratio of the plants. Ratio diagrams for all four treatments (Fig. 3) indicated stable coexistence through the season.

Discussion

The transect data show a significant nonrandom segregation between *Eleocharis* and *Juncus*. Possible underlying mechanisms that could contribute to nonrandom community structure include clonal growth form, patchy environ-

ment, and competition (Pielou 1977). However, the experimental results give no strong evidence of interference between *Eleocharis* and *Juncus*. In pure stands both species respond similarly to the environmental manipulations. These pure stand responses are independent of initial planting ratio, and provide a basis for comparing results in mixtures. Individuals of each species react more negatively to conspecifics than to individuals of the other species. This response is most pronounced at high density. Such strong negative density dependence is required for stable coexistence of competitors in community matrix models (May 1981).

Our results conclusively demonstrate that any effects of neighbors are much smaller than interspecific differences in growth, or effects on growth of density, light intensity, or substrate composition. If competitive exclusion influences natural stands of *Eleocharis* and *Juncus*, then elimination of one competitor must occur within the span of a growing season, since rosette densities of both species decrease substantially under winter ice cover. We found no evidence of interspecific interference under any environmental treatment in experiments that lasted nearly one growing season. Effects of environmental treatments, however, were pronounced. Therefore, environmental variation apparently outweighs interspecific interference in determining abundance of *Juncus* and *Eleocharis* in natural associations.

A single replacement series constrains density to a single initial value, and yields no information on the effects of density on competition (Inouye and Schaffer 1981). We attempted to rectify this shortcoming by doing experiments at two densities. In pot experiments involving clonal perennials, high density treatments may crowd plants more than they are crowded in nature, in contrast to experiments on annuals sown from seed where self-thinning during growth prevents interspecific contacts from persisting at unnaturally high density. The high mortality observed in our high density treatment may be the result of an unnaturally high initial density. However, despite the extremely small neighbor to neighbor distances, there was no evidence of interspecific difference in mortality rates. In replacement series studies of clonal perennials, we suggest the use of two or more densities at or below field density.

The response of the two species in the shading treatment indicates that *Eleocharis* is more tolerant of shade, even though the interaction between the species is not affected by shading. Light intensity often limits macrophyte growth and distribution (Jupp and Spence 1977; Moeller 1978; Titus and Adams 1979). The greater shade tolerance of *Eleocharis* correlates with its broader distribution in Wisconsin, which includes lakes that are more turbid than lakes that support both *Juncus* and *Eleocharis* (Swindale and Curtis 1957).

Our experimental results concur with several phytosociological studies of lake communities (Moeller 1975; Swindale and Curtis 1957; Johnsen 1978) which show that *Juncus* and *Eleocharis* commonly co-occur at the 0 to 2 m depth zone in oligotrophic lakes. Our results indicate that they are nonrandomly intermingled and capable of stable coexistence under a variety of different environmental conditions. The mechanism of response to neighbors that permits stable coexistence awaits explanation. Inferences about the mechanism of competition or coexistence require measurements of physiological or morphological responses of individual plants to changes in neighbor relationships.

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