

**DENSITY-DEPENDENT GROWTH INTERACTIONS BETWEEN
ELEOCHARIS ACICULARIS (L.) R. & S. AND *JUNCUS*
PELOCARPUS FORMA *SUBMERSUS* FASSETT**

N.J. McCREARY¹ and S.R. CARPENTER²

¹*Lafayette College, Easton, PA 18042 (U.S.A.)*

²*University of Notre Dame, Notre Dame, IN 46556 (U.S.A.)*

(Accepted for publication 10 September 1986)

ABSTRACT

McCreary, N.J. and Carpenter, S.R., 1987. Density-dependent growth interactions between *Eleocharis acicularis* (L.) R. & S. and *Juncus pelocarpus* forma *submersus* Fassett. *Aquat. Bot.*, 27:229-241.

Interspecific and intraspecific interactions were examined in *Eleocharis acicularis* (L.) R. & S. and *Juncus pelocarpus* forma *submersus* Fassett, two rhizomatous perennial plants which occur in the littoral zones of many temperate oligotrophic lakes. Reciprocal replacement series experiments were established in Roach Lake, U.S.A., at 4 ratios and 3 densities during the 1982 and 1983 growing seasons. Changes in biomass and in a variety of morphological characters were measured. Although the species did not differ in biomass change, *Eleocharis* produced more rosettes, longer rhizomes and more new photosynthetic structures in the first season than did *Juncus*. Effects of neighbors, regardless of species, were more important than interspecific interactions. Growth interactions between these species were competitively neutral. Differences between *Eleocharis* and *Juncus* growth dynamics lead to contrasting clonal structures that facilitate coexistence. The results would not have been interpretable without detailed, plant-by-plant morphological data. Such detailed structural analysis may be essential in studies of interspecific interactions among macrophytes.

INTRODUCTION

Zonation of aquatic plants with depth is commonly attributed to interspecific competition along the complex environmental gradient from shallow to deep water within lakes (Hutchinson, 1975). Since multispecies mixtures in apparently homogeneous depth zones are common (Carpenter and Titus, 1984), there are ample opportunities for interspecific interactions. A few studies of neighbor interactions in aquatic plant communities have detected interspecific and/or intraspecific neighbor effects (Titus and Adams, 1979; Grace and Wetzel, 1981; Agami and Waisel, 1985). However, Spence (1982) noted

that effects on depth zonation of physico-chemical factors were much better known than effects of interactions with neighbors.

We have studied the interactions of two morphologically similar species which are commonly associated in shallow waters of oligotrophic lakes: *Eleocharis acicularis* (L.) R. & S. and *Juncus pelocarpus* forma *submersus* Fassett (hereafter referred to by generic names). Lakes that contain either of these species usually contain both (Swindale and Curtis, 1957), and they are commonly found in the same depth zone (Moeller, 1975; Johnsen, 1978; Keddy, 1984; Carpenter and Titus, 1984). Morphologically, these rhizomatous, perennial, rosulate evergreen plants are quite similar to one another (Fassett, 1957). Because they are closely associated in habitats that have low concentrations of dissolved nutrients (Swindale and Curtis, 1957; Moeller, 1975), they provide a promising system for studies of interspecific competition. However, an earlier study did not detect interspecific effects on biomass gain of *Eleocharis* and *Juncus*, although intraspecific density-dependent effects were severe (McCreary et al., 1983).

This study was designed to determine both intraspecific and interspecific effects of neighbors on overall growth and several morphological characters (e.g. leaf number, rosette number, rhizome length) of *Eleocharis* and *Juncus*. Reciprocal replacement series (de Wit, 1960), which determine interspecific effects, were carried out at 3 densities. Use of multiple densities allowed us to detect intraspecific effects, or density-dependent competition. To investigate possible neighbor effects on ability to overwinter and grow the following summer, these experiments were harvested after one year and again after two years.

MATERIALS AND METHODS

Study area

Roach Lake is a 36-ha oligotrophic, soft water lake (Secchi depth 3.7 m, alkalinity 0.0–0.2 meq l⁻¹) within the University of Notre Dame Environmental Research Center in Gogebic County MI (Section 10 of T44N R42W) and Vilas County, WI (Section 7 of T43N R8E), U.S.A. Watershed geology, general limnology and submersed flora are described in detail elsewhere (McCreary et al., 1983; Carpenter and McCreary, 1985). The study site was located on a shore of northern, uniform exposure, with a gradually sloping bottom. It was accessible to divers, but protected from human disturbance. The site was populated with both species, and was near a site where plants in pots could overwinter, protected from ice disturbance.

Experimental design

The experiment was a five-way mixed model factorial design applied to plants in pots. The four fixed effects were species, density, ratio and year, and the

random effect was depth. This experimental design is equivalent to 24 reciprocal replacement series experiments, each including 5 ratios of 2 species, carried out at 3 densities and 4 depths for 2 time periods. Reciprocal replacement series adapted for use with submersed perennial plants in situ (McCreary and Carpenter, 1983) were established at each of 3 interplant spacings to manipulate density: full spacing of 1 cm per plant, approximating observed field density (McCreary et al., 1983); half spacing of one plant every 2 cm; and quarter spacing of one plant every 4 cm. The design combined individual plants of the 2 species ('E' for *Eleocharis*; 'J' for *Juncus*) in 5 mixtures at the higher 2 densities—20E:0J, 15E:5J, 10E:10J, 5E:15J and 0E:20J. At the lowest density, pots could accommodate only 10 individuals and the following mixtures were used: 10E:0J, 8E:2J, 5E:5J, 2E:8J and 0E:10J. Each species—ratio—density—year combination was replicated four times. Since growth rates of plants vary with increasing depth, these replicate pots were randomized in blocks along depth contours to remove any error variance due to depth (Sokal and Rohlf, 1981). A total of 120 pots of all combinations of species, ratio, density and depth were established in May 1982. Sixty pots were harvested in August 1982, and the remaining 60 in August 1983.

Experimental execution

Plastic pots (12.5 cm diameter \times 9 cm deep, with a 2.5-cm lip) were assembled in the laboratory. Five cm of coarse gravel were placed in the perforated bottom of each pot, and covered with 3 cm of sediment obtained from Roach Lake using an Ekman dredge. Pots were topped with 1 cm of washed sand, obtained from the 0.5-m depth contour of Roach Lake, which was used to anchor plants in the sediment. Plants were collected from 0.5–2.0 m in Roach Lake by snorkelers and returned to the laboratory, where they were sorted and washed clean of debris for use as soon as possible. Care was taken to use plants of relatively uniform size and healthy appearance. Initial measurements were made on lightly blotted plants.

A plexiglas template was used to space experimental plants in a regular hexagonal pattern. In addition, border plants were placed in the pots around the perimeter of the experimental population, at the same density and pattern. This border population helped to reduce unwanted edge effects on experimental plants (McCreary et al., 1983), and standardized plant-to-plant contacts (van Andel and Dueck, 1982).

Once assembled, pots were transported in water to the lake. Divers using SCUBA placed the replicate pots in the lake in blocks from 0.9 to 1.3 m depth. The slope of the littoral zone just accommodated the 4 depth blocks. Pots were pushed into the lake bottom so that the pot sediment surface matched the lake sediment surface, with the pot lip extending above the sediment. The pots were assembled 17–22 May 1982, and experiments were begun 19–23 May 1982. The

site was visited every 2–3 weeks to remove debris from pots by hand, and to clip nearby floating-leaved *Sparganium fluctuans* (Morong) Robinson, which might otherwise have shaded the pots.

Sixty pots (3 densities \times 5 ratios of 2 species \times 4 depth replicates) were harvested 20–21 August 1982. Pots were returned to the laboratory, where each experimental plant was recovered using the template. These plants were removed with roots and rhizome systems intact, rinsed clear of sediment with lake water, placed on labelled herbarium paper for pressing and air-drying and subsequent detailed measurements (see below). In this way, the growth of each individual plant could be followed.

The remaining 60 pots were relocated in August 1982 to a depth of 2.0 — 2.5 m to prevent possible damage by ice during the winter. On 17 May 1983, pots were returned to their original sites at the 0.9–1.3-m depth contour, and harvested by the same method on 22–23 August 1983.

Data analysis

Survivorship percentages were calculated for each species in each pot. Percentages were based upon recovered live plants upon harvest relative to the number of initial plants. Several measurements were made on each individual plant that survived the experiment. The term “photosynthetic unit” refers to a leaf of *Juncus* or a leafless photosynthesizing stem of *Eleocharis*. A dry mass/fresh mass ratio, based on a separate sample of 50 field-collected plants, was used to convert initial fresh mass to initial dry mass, and calculate net gain or loss of dry mass per living plant. The ratio of dry mass/fresh mass \pm standard error was 0.0923 ± 0.0053 for *Juncus* and 0.0869 ± 0.0036 for *Eleocharis*. Other measurements included length of rhizome produced in cm per plant, change in number of photosynthetic units on the original rosette, change in total number of photosynthetic units produced in any plant, number of new rosettes produced and number of photosynthetic units produced on new rosettes. Since flowering in submersed populations of *Eleocharis* and *Juncus* from 1979 to 1984 was not observed, biomass allocation to structures for sexual reproduction was zero.

For statistical analyses, the following ratios were used to denote representation in mixture: 0.25, 0.5, 0.75 and 1.0 at full and half spacing, and 0.2, 0.5, 0.8 and 1.0 for quarter spacing. Analyses of variance were computed following rules for mixed-model factorial designs specified by Zar (1974, pp. 333–334). Two different analyses of variance were performed. (1) Data from ratios 0.2, 0.25, 0.75 and 0.8 were deleted to produce a complete factorial design with 2 ratios (0.5 and 1.0), 3 densities, 2 species and 2 years. In this ANOVA, density and its interactions could be analyzed over the full range of densities. (2) Data were divided into 2 subsets, with ratios consistent within each. The first subset, all low density (quarter spacing) pots, was analyzed for effects of species, ratio,

TABLE 1

Results of ANOVA for seven responses measured; only main effects are presented. *F* values and degrees of freedom are indicated. All values based on measures per individual plant, except % survivorship per pot¹

Dependent variables	Independent variables		
	Species	Density	Ratio
Year 1			
% Survivorship per pot	10.9928 1.3*	4.8989 2.6ns	0.3742 1.3ns
Change in dry mass of plants (mg)	0.0658 1.3ns	6.3759 2.6*	20.1374 1.3**
Change in number of units on original	11.0925 1.3*	6.1275 2.6*	0.4494 1.3ns
Length of rhizome produced (cm)	22.0103 1.3**	1.0976 2.6ns	0.5602 1.3ns
Number of new rosettes produced	36.4306 1.3***	2.7786 2.6ns	2.0410 1.3ns
Change in the total units produced	5.0627 1.3ns	6.3232 2.6*	1.2221 1.3ns
Year 2			
% Survivorship per pot	2.7410 1.3ns	1.5537 2.6ns	4.1951 1.3ns
Change in dry mass of plants (mg)	7.4847 1.3ns	2.1232 2.6ns	0.7428 1.3ns
Change in number of units on original	37.0780 1.3***	0.6104 2.6ns	3.2213 1.3ns
Length of rhizome produced (cm)	15.8948 1.3*	2.1867 2.6ns	0.8120 1.3ns
Number of new rosettes produced	42.0065 1.3***	1.6104 2.6ns	0.0815 1.3ns
Number of new units on new rosettes	36.7803 1.3***	2.3934 2.6ns	1.6082 1.3ns
Change in total units produced	14.6032 1.3*	1.3405 2.6ns	0.4199 1.3ns

¹**P* = 0.05–0.025; ***P* = 0.025–0.01; ****P* = 0.01–0.005; ns = not significant.

year and their interactions. The second subset, all pots at higher densities, was analysed for the same effects, plus effects of density and interactions.

Survivorship data were transformed (arcsine square root) and sums of squares were weighted by the initial number of plants (Gilbert, 1973). The approximate normality of residuals from all ANOVAs was confirmed using normal probability plots (Sokal and Rohlf, 1981). Total yield response curves can indicate the type and outcome of interaction in a reciprocal replacement series (Kahn et al., 1975). One-way ANOVA tested for significant effects of ratio on total combined yield of the species.

RESULTS

The biological inferences from both analyses of variance were identical. To simplify presentation, only results from the first analysis are presented here (Table 1). The full five-way ANOVA model showed no significant effects due

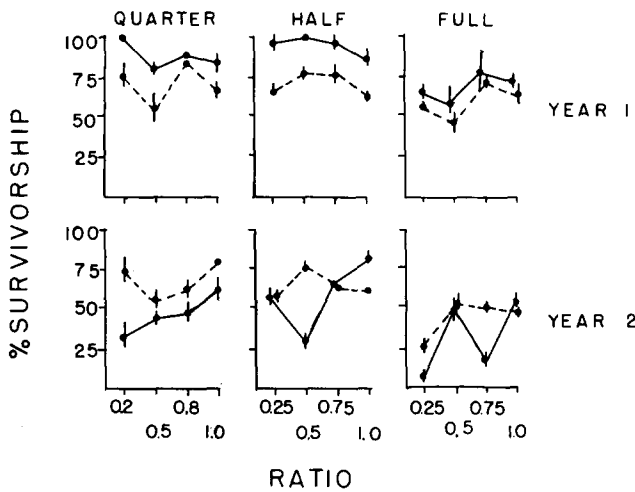


Fig. 1. % Survivorship versus ratio for 1 and 2 years at quarter, half and full spacing. *Eleocharis* is indicated with a broken line, *Juncus* with a solid line. Standard errors are indicated where larger than the data point ($n=3$ or 4).

to year for any of the response variables measured. However, year interacted strongly with other independent variables, because the effects of these variables were different in the 2 growing seasons. Therefore, it is more informative to examine results for each year individually. All differences noted are significant at a probability of 0.05 or less.

Survivorship varied between species in each year (Fig. 1). *Juncus* survivorship exceeded that of *Eleocharis* in Year 1, but *Eleocharis* survivorship was higher in Year 2. Change in dry mass per living plant (Fig. 2) was extremely variable. Both species showed negative density-dependent responses in Year 1, but those density effects were not significant after Year 2. The ratio effect in Year 1 reflected a general increase in dry mass at higher ratios.

Changes in numbers of photosynthetic units on original rosettes differed between the species in both years (Fig. 3). Density effects were significant in Year 1, but not in Year 2. In Year 1, *Eleocharis* responded unimodally, losing the fewest photosynthetic units at intermediate density. *Juncus* did not respond strongly to density.

Variables describing development of new, vegetatively produced rosettes showed several consistent trends. Length of rhizome produced (Fig. 4) and number of new rosettes produced (Fig. 5) both differed between species. *Eleocharis* produced longer rhizomes with more new rosettes than did *Juncus*. Photosynthetic units produced on new rosettes (Fig. 6) showed more pronounced trends, with *Eleocharis* producing more new photosynthetic units than *Juncus* in both years.

Changes in total photosynthetic units produced (new units on original

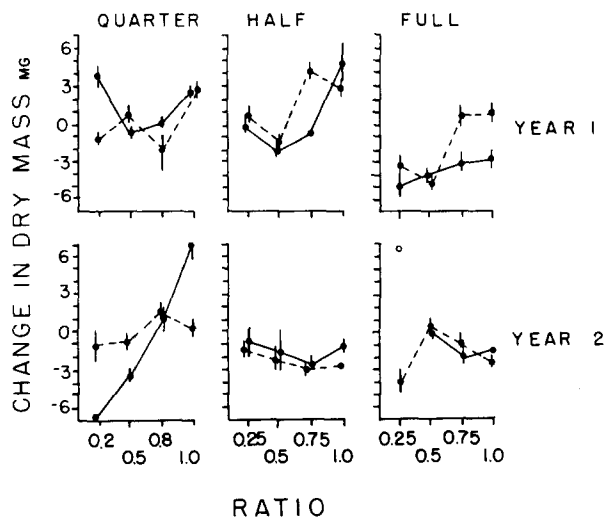


Fig. 2. Change in dry mass (mg) per plant versus ratio. Open circle indicates $n=1$. Layout and symbols as in Fig. 1.

rosette, plus units on new rosettes, minus loss of units on original) paralleled trends in new rosette production (Fig. 7). Both species responded negatively to increased density in Year 1. A species—density interaction in Year 2

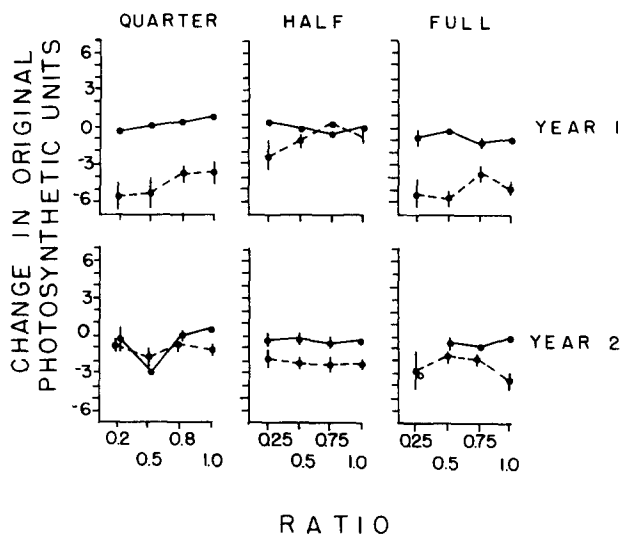


Fig. 3. Change in photosynthetic units on the original rosette versus ratio. Layout and symbols as in Fig. 1.

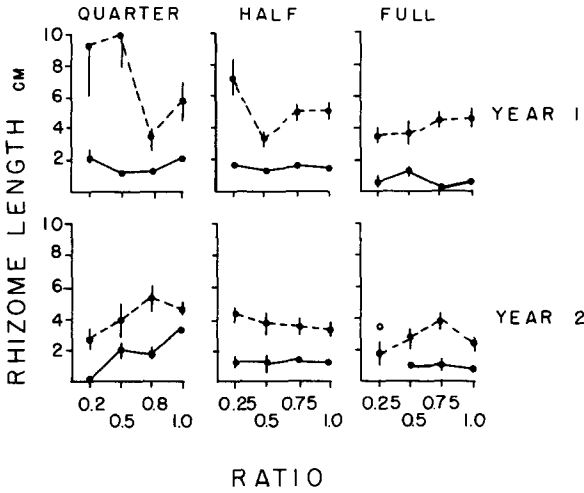


Fig. 4. Length of rhizome produced by original rosette (cm) versus ratio. Layout and symbols as in Fig. 1.

($F_{2,6}=8.6713$; $Pr>0.025$) indicated that the magnitude of response to density of *Eleocharis* exceeded that of *Juncus*.

Total yield response curves (Fig. 8) combine information on both species to indicate the type of interaction in a reciprocal replacement series (Kahn et al., 1975). Total yield response curves did not display any trends with ratio for any density treatment. Effects of ratio on combined yield were not significant for any ratio in either year (McCreary, 1985).

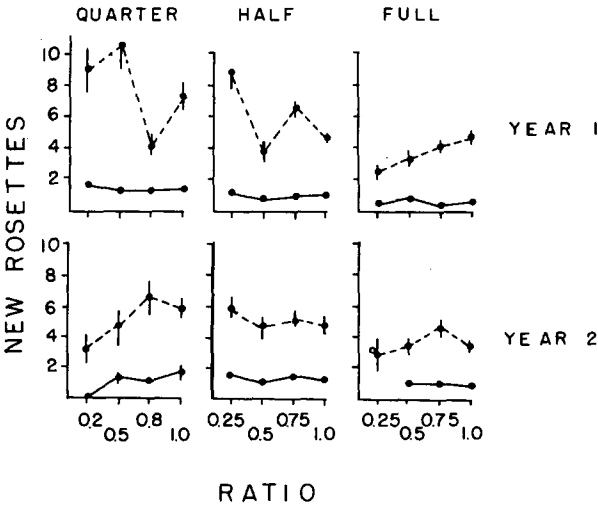


Fig. 5. Number of new rosettes produced versus ratio. Layout and symbols as in Fig. 1.

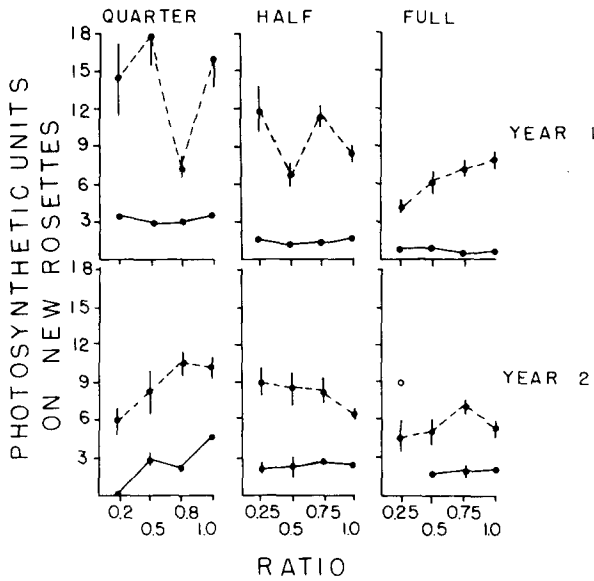


Fig. 6. Number of new photosynthetic units produced on newly formed rosettes versus ratio. Layout and symbols as in Fig. 1.

DISCUSSION

Significant negative effects of density on dry mass gain and vegetative growth occurred after 1 season. However, by the end of the second season, no density effects were evident. Mortality at high density coupled with increased growth

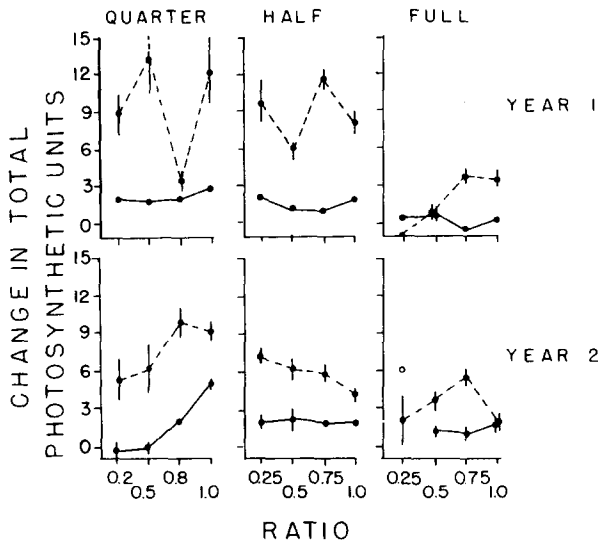


Fig. 7. Change in total number of photosynthetic units versus ratio. Layout and symbols as in Fig. 1.

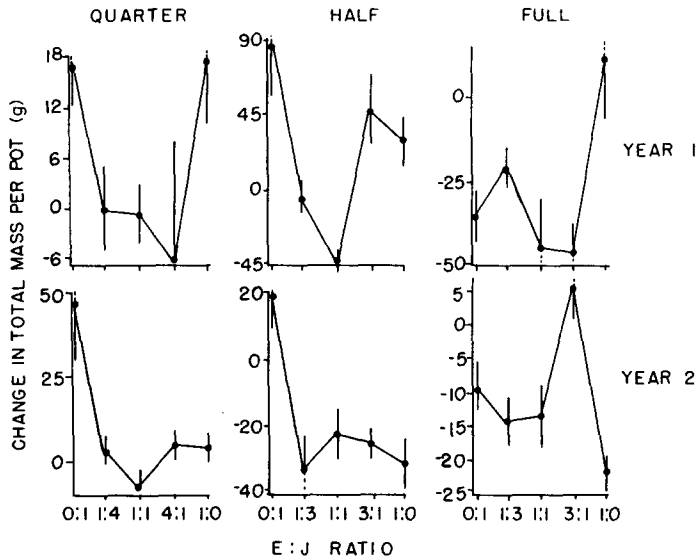


Fig. 8. Total yield response curves. Yield (g) growth per pot is plotted versus ratio for 1 and 2 years at each of 3 spacings. Mixture points are the mean of species' totals in 4 pots; pure stand points are the mean pot total ($n=3$ or 4). Standard errors are indicated where larger than data point.

at low density eliminated density effects by the end of Year 2. These results indicate convergence to a stable density within 2 years, by greater growth in pots that had low initial densities and by greater attrition in pots that had higher initial densities. Effects of ratio indicate the presence of interspecific interactions; ratio effects were evident in Year 1 only in mass gain, and not at all in Year 2.

Outcomes of a reciprocal replacement series (Kahn et al., 1975) include the following possible mechanisms: (1) insufficient density to cause interference; (2) equal or neutral mixture; (3) competitive displacement; (4) negative interaction (e.g. allelopathy); (5) either facilitative or annidative augmentation; and (6) frequency-dependent interaction. Since density effects were significant, outcome (1) can be eliminated. Competitive displacement did not occur, and so outcome (3) can be rejected. Total combined yield response curves did not indicate a positive stimulus or a ratio effect, rendering outcome (5) an unlikely mechanism. No systematic frequency dependence was evident, eliminating outcome (6).

Negative effects (outcome 4) might be an expected outcome in our experiment, since studies of *Eleocharis acicularis* and *E. coloradoensis* attribute elimination of *Potamogeton* sp., *Elodea* sp. and *Zannichellia palustris* L. to allelochemicals secreted by *Eleocharis* (Frank and Dechoretz, 1980; Yeo and Thurston, 1984). However, these greenhouse experiments studied the ability

of other species to invade *Eleocharis* lawns; *Eleocharis* cultures were established and maintained 3–4 months prior to introduction of a target species. These experiments were additive designs, and effects due to the presence of a neighbor of a different species were confounded by effects due simply to more neighbors present, regardless of species (Harper, 1977). Replacement series designs are not subject to this confounding, and preclude pre-emption of space by using even-aged populations introduced simultaneously. This approach is of particular importance for plants such as *Eleocharis* and *Juncus* which spread almost entirely by vegetative growth. In addition, species more commonly associated with *Eleocharis*, such as *Juncus*, might better tolerate any phytotoxin than the more robust species above, which are not commonly associated with *Eleocharis* (Swindale and Curtis, 1957). In sum, our results do not support a detrimental, allelopathic interaction (outcome 4).

Our data indicate a neutral interaction (outcome 2) between *Eleocharis* and *Juncus* in Roach Lake, supporting those of McCreary et al. (1983). These plants respond primarily to the number and proximity of neighbors, but are not sensitive to the species of neighbor present regardless of its distance.

Although morphologically very similar, *Eleocharis* and *Juncus* exhibited substantial differences in growth patterns at the module-level. Biomass gain is not necessarily the most sensitive or botanically significant index of plant responses to neighbors (White, 1984), especially in clonal perennial herbs such as *Eleocharis* and *Juncus*. The interspecific differences in vegetative growth responses occurred during both growing seasons, while biomass differences occurred only in the first season. Therefore, the species remained distinctly different in the pattern of module propagation, while the genet population came to stable levels of density and biomass.

The modular responses of these species generate differing architectures. The classification of “guerilla” and “phalanx” species has been used to describe these relative differences (Harper, 1977; Lovett-Doust, 1981). Phalanx species, such as *Juncus*, have short horizontal internodes, with photosynthetic units packed in a clump. In contrast, guerilla species such as *Eleocharis* bear rosettes spaced on longer internodes. It is variation in the architecture of these perennial herbs that determines the type, degree and consequences of neighbor contacts (Harper, 1981; Watson and Cook, 1982; Pavlick, 1983; Bulow-Olsen et al., 1984). Had we not measured modular responses, we would have missed these architectural differences between *Eleocharis* and *Juncus*. The differences in architecture evident in these experiments are related to the common and stable association of these species in this lake, and perhaps in other north temperate oligotrophic lakes.

ACKNOWLEDGEMENTS

Appreciation is given to A. Bergquist, J. Chaney, M.L. Jaynes and J. Latino for technical assistance, to J.E. Titus and two anonymous reviewers for com-

ments on the manuscript, and to O.J. and S. Stewart for hospitality and general assistance. This research, which represents a part of the dissertation work of N.J.M., was supported by grants from the University of Notre Dame Faculty Research Fund to S.R.C., and by grants to N.J.M. from Sigma Xi, Indiana Academy of Science and the Zahm Research Travel Fund. This is a contribution from the University of Notre Dame Environmental Research Center.

REFERENCES

- Agami, M. and Waisel, Y., 1985. Inter-relationships between *Najas marina* L. and 3 other species of aquatic macrophytes. *Hydrobiologia*, 126: 169-174.
- Bulow-Olsen, A., Sackville-Hamilton, N.R. and Hutchings, M.J., 1984. A study of growth form in genets of *Trifolium repens* L. as affected by intra- and inter-plant contacts. *Oecologia*, 61: 383-387.
- Carpenter, S.R. and McCreary, N.J., 1985. Effects of fish nests on pattern and zonation of submersed macrophytes in a softwater lake. *Aquat. Bot.*, 22: 21-32.
- Carpenter, S.R. and Titus, J.E., 1984. Composition and spatial heterogeneity of submersed vegetation in a softwater lake in Wisconsin. *Vegetatio*, 57: 153-165.
- De Wit, C.T., 1960. On competition. *Versl. Landbouwk. Onderz.*, 66: 1-82.
- Fassett, N.C., 1957. *A Manual of Aquatic Plants*. University of Wisconsin Press, Madison, 405 pp.
- Frank, P.A. and Dechoretz, A., 1980. Allelopathy in dwarf spikerush (*Eleocharis coloradoensis*). *Weed Sci.*, 18: 499-505.
- Gilbert, N., 1973. *Biometrical Interpretation*. Clarendon, Oxford, 125 pp.
- Grace, J.B. and Wetzel, R.G., 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies. *Am. Nat.*, 118: 463-474.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, New York, 892 pp.
- Harper, J.L., 1981. The concept of population in modular organisms. In: R.M. May (Editor), *Theoretical Ecology*. Sinauer, Sunderland, pp. 53-77.
- Hutchinson, G.E., 1975. *A Treatise on Limnology*. Vol. III. Wiley, New York, 660 pp.
- Johnsen, P.S., 1978. The littoral zone of Pine Lake, Wisconsin: Patterns and limiting factors of macrophyte distribution. MS Thesis, University of Wisconsin-Madison, 91 pp.
- Kahn, M.A., Putwain, P.D. and Bradshaw, A.D., 1975. Population inter-relationships. 2. Frequency dependent fitness in *Linum*. *Heredity*, 34: 145-163.
- Keddy, P.A., 1984. Plant zonation on lakeshores in Nova Scotia: a test of the resource specialization hypothesis. *J. Ecol.*, 72: 797-807.
- Lovett-Doust, L., 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus*). I. The dynamics of ramets in contrasting habitats. *J. Ecol.*, 69: 743-755.
- McCreary, N.J., 1985. Competition and coexistence in two vegetative freshwater perennials: *Eleocharis acicularis* (L.) R. & S. and *Juncus pelocarpus* forma *submersus* Fassett. Ph.D. Thesis, University of Notre Dame, Indiana, 172 pp.
- McCreary, N.J. and Carpenter, S.R., 1983. Competition among submersed perennial plants: Use of reciprocal replacement series in situ. In: Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, The Netherlands, pp. 134-138.

- McCreary, N.J., Carpenter, S.R. and Chaney, J.E., 1983. Coexistence and interference in two submersed freshwater perennial plants. *Oecologia*, 59: 393-396.
- Moeller, R.E., 1975. Hydrophyte biomass and community structure in a small oligotrophic New Hampshire lake. *Verh. Int. Ver. Limnol.*, 19: 1004-1012.
- Pavlick, B.M., 1983. Nutrient and productivity relations of the dune grasses *Ammophila arenaria* and *Elymus mollis*. III. Spatial aspects of clonal expansion with reference to rhizome growth and the dispersal of buds. *Bull. Torr. Bot. Club*, 110: 271-279.
- Sokal, R.R. and Rohlf, F.J., 1981. *Biometry*. Freeman, San Francisco, 859 pp.
- Spence, D.H.N., 1982. Zonation of plants in freshwater. *Adv. Ecol. Res.*, 12: 37-126.
- Swindale, D.A. and Curtis, J.T., 1957. Phytosociology of the larger submerged plants in Wisconsin lakes. *Ecology*, 38: 397-407.
- Titus, J.E. and Adams, M.S., 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. *Oecologia*, 40: 272-286.
- Van Andel, J. and Dueck, T., 1982. The importance of the physical pattern of plant species in replacement series. *Oikos*, 39: 59-62.
- Watson, M.A. and Cook, C.S., 1982. The development of spatial pattern in clones of an aquatic plant, *Eichhornia crassipes* Solms. *Am. J. Bot.*, 69: 248-253.
- White, J., 1984. Plant metamerism. In: O. Dirzo and J. Sarukhan (Editors), *Perspectives on Plant Population Ecology*. Sinauer, Sunderland, pp. 15-47.
- Yeo, R.R. and Thurston, J.R., 1984. The effect of dwarf spikerush (*Eleocharis coloradoensis*) on several submersed aquatic weeds. *J. Aquat. Plant Manage.*, 22: 52-56.
- Zar, J.H., 1974. *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, NJ, 620 pp.