

## MEASURING DIFFUSE COMPETITION ALONG AN ENVIRONMENTAL GRADIENT: RESULTS FROM A SHORELINE PLANT COMMUNITY

SCOTT D. WILSON\* AND PAUL A. KEDDY

Department of Biology, University of Ottawa, Ottawa, Ontario K1N 6N5, Canada

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The ecological literature is rich with studies of competition in plant communities. Most experimental studies are limited by necessity to the examination of pairwise interactions within a small group of species (e.g., Putwain and Harper 1970; Sharitz and McCormick 1973; Grace and Wetzel 1981; Fowler 1982; Silander and Antonovics 1982; Rabinowitz et al. 1984). In nature, however, an individual may compete with a constellation of species in various combinations and densities; that is, an individual is often faced with diffuse competition (MacArthur 1972). In spite of its importance in natural communities, diffuse competition has received almost no experimental attention (Davidson 1985).

Current ecological models describing life history strategies and species diversity are based on the untested assumption that the intensity of diffuse competition varies with the amount of standing crop (Grime 1979), disturbance (Connell 1978; Huston 1979), or grazing (Lubchenco and Gaines 1981). Measuring diffuse competition simultaneously at several locations along an environmental gradient would allow explicit testing of this assumption and its associated models.

Our study had three objectives: to present a method for measuring diffuse competition along an environmental gradient; to use this method to test whether diffuse competition is correlated with the amount of standing crop in a natural plant community; and to test whether diffuse competition is correlated with an important environmental gradient underlying the community.

### METHODS

#### *Measuring Diffuse Competition along a Gradient*

We present a general method for measuring diffuse competition along an environmental gradient. Several locations are chosen along the gradient. Each location is divided in half, one half cleared of all aboveground biomass, and ramets of several species planted in each half. The density of transplanted ramets

\* Present address: Department of Botany, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada.

should be so low that shoots do not shade each other and belowground parts do not come into contact. Ramets are allowed to grow for one or more growing seasons before the harvesting of aboveground and belowground biomass. The biomass accumulated by transplanted ramets in cleared and uncleared plots is compared in order to calculate diffuse competition at each location:

$$DC = \left\{ \sum_{i=1}^n [(\bar{C}_i - \bar{U}_i)/\bar{C}_i] \right\} n^{-1},$$

where  $DC$  is a measure of diffuse competition,  $\bar{C}_i$  is the mean dry weight of species  $i$  in the cleared treatment;  $\bar{U}_i$ , the mean dry weight of the species in the uncleared control; and  $n$ , the number of transplanted species. The difference between the dry weight of ramets in cleared and uncleared treatments is divided by the mean dry weight of the species in cleared treatments to account for the relative size of each species. The correlation between diffuse competition and some measure of the environmental gradient is then calculated.

### *The Environmental Gradient*

The gradient chosen for study was the gradient of exposure to wave action that runs parallel to the waterline of small lakes. Horizontal variation in the abundance of plant species along the exposure gradient has been described by Pearsall (1920), Thunmark (1931), Aiken and Gillett (1974), Keddy (1983), and Wilson and Keddy (1985a). Exposure is a multivariate gradient including both stress and disturbance (in the sense of Grime 1979). Disturbance is produced by the direct effect of wave action removing more biomass from exposed shores than from sheltered shores. Stress is produced on exposed shores by wave action creating soils with low organic-matter content, low nutrient concentrations, and coarse particle sizes. These abiotic factors are significantly correlated with the exposure to wave action (Keddy 1985). The exposure gradient is characterized at one end by wave-washed, sparsely vegetated, nutrient-poor beaches and at the other by sheltered, densely vegetated, nutrient-rich bays. In this study, the position along the exposure gradient was quantified by measuring the organic-matter content of the soil (Wilson and Keddy 1985a).

### *Diffuse Competition*

Diffuse competition was measured at eight locations representing the range of standing crop on the shore of Axe Lake, Ontario (Keddy 1983). Each location consisted of a cleared treatment plot and an adjacent uncleared control plot. Each plot comprised 30 pots (each 15 cm in diameter, 12 cm deep, with 8 1-cm<sup>2</sup> drainage holes) in 6 rows of 5 pots each, installed by removing a sediment core the size of a pot, putting it into a pot, and returning the potted soil to the sediment. Pots excluded invading rhizomes and allowed a controlled harvesting of belowground biomass. All aboveground vegetation was then removed from the treatment plots and from a 15-cm border surrounding the cluster of pots. Any emerging shoots were removed over the course of the experiment.

In each plot, we planted 10 ramets each of three shoreline species, *Juncus*

*pelocarpus* E. Meyer., *Rhynchospora fusca* (L.) Ait. f., and *Lysimachia terrestris* (L.) BSP. (Gleason and Cronquist 1963). All species are found over the entire range of the exposure gradient (Wilson and Keddy 1985a). *Juncus*, a small graminid (5–15 cm tall) grows in dense mats and is most often found on exposed, sandy shores; *Rhynchospora* is a rhizomatosely spreading graminid (15–40 cm tall) distributed evenly along the exposure gradient; and *Lysimachia* is a tall (40–80-cm), leafy, rhizomatous herb most often found on sheltered shores with high organic-matter content in the soil. Species were chosen for their different morphologies. Ramets were collected on July 3, planted July 3–6, and harvested September 6, 1984. The experiment was harvested after a single growing season because in the following year it would not have been possible to distinguish between shoots arising from transplanted rhizomes and shoots of the same species that occurred naturally in the control plots.

The position of each experimental location on the exposure gradient was measured by determining the mean organic-matter content (Dean 1974) of six soil samples (each 3.5 cm in diameter, 5 cm deep) from each location.

Standing crop was harvested from a 0.2-m × 0.2-m quadrat adjacent to each plot on August 25, 1984. Standing-crop samples were dried to constant weight, and the mean standing crop was determined for each location.

The correlation between *DC* (measure of diffuse competition) and standing crop for all locations was tested using Pearson's *r* after arcsine transformation of *DC*. Although *DC* calculated for three species together gives a general measure of diffuse competition, *DC* can also be calculated for each species individually to test for among-species differences in responses. This can be done by calculating *DC* as in the equation for each species and then testing for a correlation between *DC* and standing crop.

#### *Standing Crop and Exposure*

We tested the hypothesis that standing crop is related to the exposure gradient in order to interpret the experimental results with reference to abiotic factors. The shoreline of Axe Lake was sampled at 20-m intervals along the waterline during August 17–21, 1984 ( $N = 83$ ). At each interval, standing crop was harvested from a quadrat 0.2 m by 0.2 m, and a soil sample was taken for analysis of the organic-matter content. The correlation between standing crop and the organic-matter content of the soil was tested using Pearson's *r*.

#### RESULTS

Diffuse competition was significantly correlated with standing crop ( $r = 0.76, P = 0.02$ ) for all transplanted species considered together. Figure 1 shows that diffuse competition increases with community standing crop.

The relationship between diffuse competition and standing crop varied when the transplanted species were considered separately. *Lysimachia terrestris* showed no correlation between *DC* and standing crop ( $r = 0.04, P = 0.46$ ), *Juncus pelocarpus* showed a weak correlation ( $r = 0.57, P = 0.07$ ), and *Rhynchospora fusca* showed a strong correlation ( $r = 0.80, P = 0.01$ ).

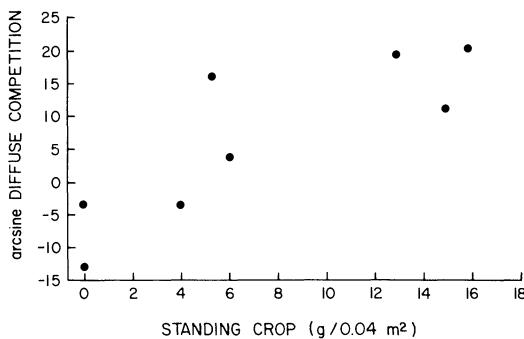


FIG. 1.—The relationship between diffuse competition, calculated as in the equation, and standing crop on the shoreline of Axe Lake, Ontario. The correlation is significant ( $r = 0.76$ ,  $P = 0.02$ ).

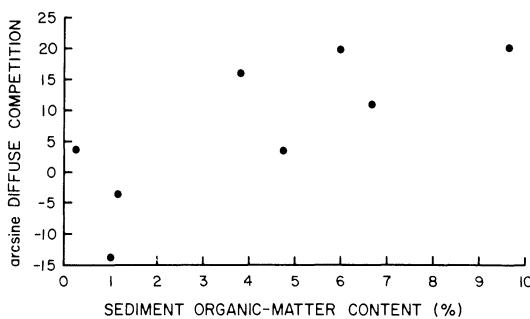


FIG. 2.—The relationship between diffuse competition and organic-matter content of the soil on the shore of Axe Lake. Organic content is low on exposed shores (left) and high on sheltered shores (right). The correlation is significant ( $r = 0.76$ ,  $P = 0.02$ ).

Diffuse competition is also correlated significantly with sediment organic matter ( $r = 0.76$ ,  $P = 0.02$ ) for the three transplanted species considered together. Figure 2 shows that diffuse competition is most intense in relatively undisturbed habitats with high nutrient concentrations in the soil. Sandy shorelines, exposed to wave action and having nutrient-poor soils, had relatively low levels of diffuse competition.

Standing crop is correlated significantly and positively with the levels of soil organic matter ( $r = 0.79$ ,  $P < 0.01$ ). Figure 3 shows that standing crop is highest on sheltered shores with the most organic matter.

#### DISCUSSION

These results suggest that diffuse competition in a shoreline plant community is most important where infrequent disturbance and nutrient-rich soils result in high standing crop.

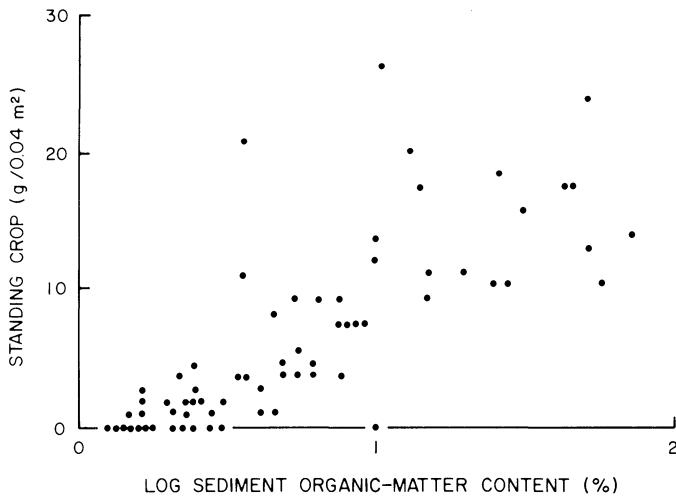


FIG. 3.—The relationship between community standing crop and organic-matter content in the soil on the shore of Axe Lake ( $r = 0.79$ ,  $P < 0.01$ ). Standing crop is lowest on exposed, sandy shores and highest on sheltered shores with organic sediments.

We have assumed that our experiment ran long enough to detect variation in diffuse competition. Transplant shock resulting from desiccation was presumably unimportant because the ramets were transplanted under water. The experiment was conducted over 65 days during the season of warmest temperatures and greatest productivity for southern Canadian wetlands (Auclair et al. 1976). Allowing the experiment to run for a second summer would probably increase the difference between plants grown in cleared and uncleared plots, producing a stronger relationship between diffuse competition and standing crop than that shown in figure 1. We also assumed that removing only aboveground biomass from cleared plots actually decreases diffuse competition. Belowground biomass remaining in the pots may continue to compete with transplanted ramets (Newman 1973). Belowground competition, if present, would cause diffuse competition to be underestimated. Although the length of the experiment and the belowground competition may affect the measurement of competition, both of these factors should have resulted in an underestimation of diffuse competition in this study. Alternatively, belowground biomass in cleared plots might have died, releasing nutrients and stimulating growth, resulting in an overestimation of diffuse competition. The production of new shoots from rhizomes and tubers in the cleared plots over the course of the experiment, however, makes this unlikely.

The relationship shown in figure 1 varies with the species used to measure diffuse competition. A species may be insensitive to variation in diffuse competition either if it is a strong competitor and seldom affected by competition or if it is a weak competitor and uniformly suppressed by all intensities of competition. For example, the large and leafy *Lysimachia terrestris* showed no correlation between

diffuse competition and standing crop. The use of different species in the experiment not only produces a general measure of diffuse competition, but also provides information on the different responses of several species to a gradient of diffuse competition.

Mutualism among individuals is suggested where the values of *DC* in figures 1 and 2 are negative. In these cases, plants grown with neighbors accumulated more biomass than those grown singly. On lakeshores, mutualism might be expected at highly exposed sites, where neighbors could provide a shelter from wave action and a stabilization of sediments. Mutualism may be tested for by determining whether the *y*-intercept of a regression line describing the relationship between diffuse competition and standing crop (fig. 1) is significantly less than 0. In this case, it was not ( $t = 1.89$ , NS; Zar 1974). Using more experimental locations might allow better tests of hypotheses concerning intercepts or curvilinearity.

A mechanism common to several current models of species diversity is the variation in the intensity of competition within a community (Grime 1973, 1979; Connell 1978; Huston 1979; Lubchenco and Gaines 1981). Connell (1983) has discussed how the importance of competition may vary spatially, but no field experiment has explicitly tested for a variation in diffuse competition along an environmental gradient. Our results corroborate the assumption that diffuse competition is inversely related to disturbance and environmental stress.

The role of exposure to wave action as an underlying control of diffuse competition is suggested by the correlation between standing crop and sediment organic content (fig. 3). Shores exposed to high amounts of wave action have low organic-matter content in the soil and low amounts of standing crop, which may result in low intensities of diffuse competition.

These results agree with those of del Moral (1983), who related the differential survival of transplants in natural vegetation to habitat productivity and competition intensity. In a greenhouse experiment, Bazzaz and Harper (1976) grew a mixture of two species in soils of high and low fertility. They found that on fertile soil, survival declined rapidly and one species was eliminated entirely, suggesting that competition was more intense under productive conditions. Experimental evidence shows that competition may be more intense in productive habitats than in unproductive environments (cf. Newman 1973; Chapin and Shaver 1985).

Although controversy has surrounded the study of competition in ecological communities (Salt 1983), our results indicate that diffuse competition may vary predictably in nature. Moreover, figures 1 and 2 suggest that the success of any particular experiment in measuring competition can depend on the environment considered. For example, field experiments with lakeshore plants have found no evidence that competition is at work in relatively disturbed or nutrient-poor habitats (McCreary et al. 1983; Titus and Stephens 1983; Wilson and Keddy 1985b; Wilson et al. 1985). In contrast, experiments in undisturbed and nutrient-rich field sites have suggested an important role for competition (Buttery and Lambert 1965; Grace and Wetzel 1981). Testing for variation in diffuse competition along environmental gradients in other plant communities may provide a more general understanding of the role of competition in nature.

## SUMMARY

We propose a method for measuring variation in diffuse competition along an environmental gradient. This approach has two advantages over pairwise-competition experiments conducted in homogeneous environments. First, it may be more realistic, since individuals in nature are usually confronted with a variety of neighbors, that is, with diffuse competition. Second, this approach allows us to test whether the variation in diffuse competition is correlated with gradients in environmental factors. We used a field experiment to test whether diffuse competition is correlated with standing crop and organic-matter content in the soil of a lakeshore plant community. Diffuse competition was correlated significantly and positively with both of these factors. Further, standing crop was correlated positively with organic-matter content in the soil, suggesting that a general measure of habitat productivity may be indirectly related to the intensity of diffuse competition. These results support models of species diversity and adaptive strategies that assume a predictable variation in the importance of competition within a community.

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## LITERATURE CITED

- Aiken, S., and J. M. Gillett. 1974. The distribution of aquatic plants in selected lakes in Gatineau Park, Quebec. *Can. Field-Nat.* 88:437–448.
- Auclair, A. N. D., A. Bouchard, and J. Pajaczkowski. 1976. Plant standing crop and productivity relations in a *Scirpus-Equisetum* wetland. *Ecology* 59:941–952.
- Bazzaz, F. A., and J. L. Harper. 1976. Relationship between plant weight and numbers in mixed populations of *Sinapsis alba* (L.) Rabenh. and *Lepidium sativum* L. *J. Appl. Ecol.* 13:211–216.
- Buttery, B. R., and J. M. Lambert. 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham broad. I. The competition mechanism. *J. Ecol.* 53:163–181.
- Chapin, F. S., III and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66:564–576.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science (Wash., D.C.)* 199:1302–1310.
- . 1983. On the prevalence and importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661–696.
- Davidson, D. W. 1985. An experimental study of diffuse competition in harvester ants. *Am. Nat.* 125:500–506.
- Dean, W. E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *J. Sediment. Petrol.* 44:242–248.

- del Moral, R. 1983. Competition as a control mechanism in subalpine meadows. *Am. J. Bot.* 70:232–245.
- Fowler, N. 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. *J. Ecol.* 70:77–92.
- Gleason, H. A., and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Willard Grant, Boston.
- Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *Am. Nat.* 118:463–474.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature (Lond.)* 242:344–347.
- . 1979. Plant strategies and vegetation processes. Wiley, Chichester, U.K.
- Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113:81–101.
- Keddy, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology* 64:331–344.
- . 1985. Wave disturbance on lakeshores and the within-lake distribution of Ontario's Atlantic coastal plain flora. *Can. J. Bot.* 63:656–660.
- Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annu. Rev. Ecol. Syst.* 12:405–437.
- MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York.
- McCreary, N. J., S. R. Carpenter, and J. E. Chaney. 1983. Coexistence and interference in two submerged freshwater perennial plants. *Oecologia (Berl.)* 59:393–396.
- Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. *Nature (Lond.)* 244:310.
- Pearsall, W. H. 1920. The aquatic vegetation of the English Lakes. *J. Ecol.* 7:163–201.
- Putwain, P. D., and J. L. Harper. 1970. Studies in the dynamics of plant populations. III. The influence of associated species on populations of *Rumex acetosa* L. and *R. acetosella* L. in grassland. *J. Ecol.* 58:251–264.
- Rabinowitz, D., J. K. Rapp, and P. M. Dixon. 1984. Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology* 65:1144–1154.
- Salt, G. W. 1983. Roles: their limits and responsibilities in ecological and evolutionary research. *Am. Nat.* 122:697–705.
- Sharitz, R. R., and J. F. McCormick. 1973. Population dynamics of two competing annual plant species. *Ecology* 54:723–740.
- Silander, J. A., and J. Antonovics. 1982. Analysis of interspecific interactions in a coastal plain community—a perturbation experiment. *Nature (Lond.)* 298:557–560.
- Thunmark, S. 1931. Der See Fiolen und seine Vegetation. *Acta Phytogeogr. Suec.* 2.
- Titus, J. E., and M. D. Stephens. 1983. Neighbor influences and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake. *Oecologia (Berl.)* 56:23–29.
- Wilson, S. D., and P. A. Keddy. 1985a. Plant zonation on a shoreline gradient: physiological response curves of component species. *J. Ecol.* 73:851–860.
- . 1985b. The shoreline distribution of *Juncus pelocarpus* along a gradient of exposure to waves: an experimental study. *Aquat. Bot.* 21:277–284.
- Wilson, S. D., P. A. Keddy, and D. L. Randall. 1985. The distribution of *Xyris difformis* along a gradient of exposure to waves: an experimental study. *Can. J. Bot.* 63:1226–1230.
- Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J.