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ABOVE- AND BELOWGROUND COMPETITION INTENSITY IN TWO CONTRASTING WETLAND PLANT COMMUNITIES[1]

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Abstract. A fundamental question in plant ecology is if and how the intensity of competition changes with productivity. This question has been the source of considerable discussion during the last two decades, yet few experiments have tested whether competition intensity changes with productivity in nature. Even fewer studies have separated competition into its above- and belowground components in the field. We used a field experiment to measure total competition intensity and its above- and belowground components in two wetlands that represent extremes in habitat productivity: an infertile sandy shoreline and a fertile bay. Transplants of *Lythrum salicaria* and *Carex crinita* were grown with no neighbors, with roots of neighbors only, and with roots and shoots of neighbors; their growth rates were used to measure competition intensity (CI). The experiment was carried out to answer the following main questions: (1) Is there a difference in total, above- and belowground competition intensity in two wetlands that differ in standing crop? and (2) Is there an effect of standing crop on total, above- and belowground competition intensity when the data from the two wetlands are combined?

Results based on the average of both species show that total and aboveground competition intensity were greater in the high standing crop wetland, but belowground competition did not differ between wetlands (CI_{TOTAL}: $P < 0.00001$, CI_{ABOVE}: $P = 0.0013$, CI_{BELOW}: $P = 0.58$). Total and aboveground competition intensity were significantly affected by standing crop in the wetlands studied but belowground competition intensity was not (CI_{TOTAL}: $P = 0.0001$, CI_{ABOVE}: $P = 0.0001$, CI_{BELOW}: $P = 0.89$). Results based on the two species separately show that species vary in their sensitivity to competition in wetland communities.

Key words: light penetration; productivity; root competition; resource competition; shoot competition; soil fertility; standing crop; wetland.

INTRODUCTION

Total competition intensity

It has long been observed that plant species composition, plant species diversity, and plant growth forms vary in nature with productivity (Whittaker 1975, Grime 1979, Tilman 1988). One fundamental question is if and how productivity influences the role of competition in determining community structure (Grime 1979, Tilman 1988, Keddy 1989, Turkington et al. 1993). Competition intensity may increase with productivity (Grime 1973, 1974, 1979, Huston 1979, Thompson and Grime 1988, Keddy 1989, 1990, Wisheu and Keddy 1992, Campbell and Grime 1992), remain constant as productivity changes (Newman 1973, Tilman 1982, 1988, Grubb 1985) or be dependent on the ratio of resource supply to demand, which may be unrelated to productivity (Taylor et al. 1990).

The results of field experiments that have tested for such patterns are contradictory (Gurevitch 1986, Wilson and Keddy 1986, Reader and Best 1989, Reader 1990, Wilson and Shay 1990, Wilson and Tilman 1991,1993, Reader et al. 1994, Belcher et al., *in press*). If one tries to compare existing field results to make generalizations, one finds that competition has been evaluated along a range of productivity gradients such as soil depth, nutrient availability, standing crop, and topography in a range of vegetation communities including alvars, mixed-grass prairies, abandoned pastures, old fields, and shorelines. In addition, the intensity of competition has been calculated using both absolute and relative equations. In recent work, competition intensity increased with productivity when calculated using absolute equations, but not when calculated using relative equations (Campbell and Grime 1992, Turkington et al. 1993, Reader et al. 1994). Results may therefore be dependent on how competition intensity was calculated (Grace 1993, 1995). There has also been a lack of consideration for whether competition intensity refers to the per gram, per plant, or per community effect of competition (Goldberg 1990, Grace 1991).

Given the importance of this problem and the contradictory results of previous experiments, we used a field phytometer experiment to measure plant competition intensity in two communities that differ in standing crop. Final standing crop is used here as an estimate of the production of the community (Chapman 1976, Whigham et al. 1978). The study was designed to answer the following main question, (1) Is mean total

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competition intensity different in two wetlands that differ in standing crop? There was natural variation in standing crop within wetlands, which resulted in overlapping standing crop values between the two wetlands. We were able to obtain a predictive and general result that focused solely on the differences in standing crop and therefore also asked, (2) Is there an effect of standing crop on total competition intensity?

The components of competition

As well as determining if and how competition intensity varies with productivity it is important to determine if and how the above- and the belowground components vary with productivity (Grime 1979, Tilman 1988). Few field experiments have separated the intensity of competition into above- and belowground components (Putz and Canham 1992, Wilson 1993*a, b,* Wilson and Tilman 1993, Belcher et al., *in press*). To date these studies have all been done in terrestrial plant communities, they have used different kinds of productivity gradients in different types of plant communities, and their results have varied. Our study therefore also asked (3) Is aboveground and belowground competition intensity different in two wetlands that differ in standing crop? and (4) Is there an effect of standing crop on aboveground competition intensity and belowground competition intensity?

The use of phytometers

A phytometer can be planted into a community and the total effect of neighboring plants on phytometer plant traits, such as relative growth rate, final biomass, survivorship, basal area, etc., can be measured. It is a realistic bioassay of competition because a plant competes with all surrounding plants simultaneously in nature and not with one plant at a time (Wilson and Keddy 1986, Keddy 1989). This method has two primary advantages. First, it provides a general and comparative approach to measuring the magnitude of competition occurring in a community. Second, it is a practical alternative to the formidable task of measuring the amount of competition between each pair of individuals or species.

In some studies it has been found that the choice of indicator species had no effect on the results (Gaudet and Keddy 1988). Others have found that the choice of indicator species affects the magnitude of competition (Wilson and Keddy 1986, DiTommasio and Aarssen 1989, Wilson 1993*b*), the relative importance of below- and aboveground competition (Putz and Canham 1992) and the importance of competition (Reader and Bonser 1993). For this reason, we decided to base our measures of competition intensity on the mean results for two common wetland species, *Lythrum salicaria* and *Carex crinita.* These wetland species were chosen because they represent two very different wetland plant guilds (Boutin and Keddy 1993), both of which typify common wetland plant morphologies. A further question posed here is whether the results are the same using two very different indicator species. The previously stated four questions are repeated for both species separately to determine whether the choice of phytometer affected the results.

METHODS

Study site

The experiment was carried out in two wetland communities at Westmeath Provincial Park (latitude 45° 47.8′, longitude 76°53.5′) which is located 110 km northwest of Ottawa, Canada. One wetland was a low standing crop wetland that was located along the shoreline of the Ottawa River. The other was a high standing crop wetland that was located in a bay of the same river.

Experimental design

A vegetation removal experiment involving introduced phytometers (Aarssen and Epp 1990) was conducted to measure competition intensity in the field. The competition intensity values obtained reflect the total effect of neighboring plants on a phytometer (Clements and Goldsmith 1924, Clements 1935, Antonovics and Primack 1982) and therefore include both interference effects and exploitative effects (Connell 1990). Thirty experimental plots, each 2 × 8 m, were established in each wetland community on 1 and 2 June 1992. Each plot was divided into four equal subplots, 2 × 2 m. The four subplots were randomly assigned to three competition treatments and a control treatment.

The four treatments were as follows: (1) Control (C) and (2) Neighbors' Roots and Shoots (NRS): These were established by leaving all natural vegetation untouched. The only difference between these two treatments was that the control subplots did not contain phytometers, whereas the neighbors' roots and shoots subplots did. (3) Neighbors' Roots (NR): This was established by using a square piece of black plastic netting to hold the shoots and leaves of the surrounding vegetation at an angle toward the outside of the subplot. The netting was of the same consistency as fishing line and had 1-cm² holes; shading effects were therefore negligible. The netting was secured with string in the center of the subplot by six 1 cm diameter aluminum rods that were arranged in two sets of three and inserted all the way into the ground. At the outside four corners of the subplot, the netting was secured with string by four 1 cm diameter aluminum rods. Holes were cut in the netting between the two sets of central rods to allow for transplanting. (4) No Neighbors (NN): This was established by clipping all standing crop at soil level (3 June–9 June) and applying a nonselective herbicide (Round Up; 38g/L glycophosphate; 500 mL in 25 L of water for 50 m²) to all shoots that were not killed by clipping. All roots were cut around the outside of the subplot to a depth of ≈30 cm.

Phytometers

The two species used as phytometers were *Lythrum salicaria* (Lythraceae) and *Carex crinita* (Cyperaceae). *Lythrum salicaria* is an introduced species that is a ruderal facultative annual and *Carex crinita,* a native species, is an interstitial tussock perennial (Boutin and Keddy 1993). Both are common wetland plants that occur at Westmeath Provincial Park. The plants were started from seed in early April at the University of Ottawa greenhouse. Prior to transplanting, 210 phytometers of each species that were most similar in size were selected from the seedlings grown. The height and the number of leaves of all 420 plants were measured. Thirty of these plants of each species were harvested, dried, and their above- and belowground biomass measured. The remaining 360 plants were transported to the field site and used in the experiment. From 12 to 14 June one phytometer of each species was planted in all competition treatment subplots (not in controls). A hole 5 cm deep and 4 cm^2 was dug, and the transplant plug was removed from the transplant pot and placed into the hole, without disturbing surrounding vegetation and soil. The phytometers were placed 25 cm from the middle of the subplot and 50 cm from one another and the transplanting process was completely randomized. Phytometer survivorship was very high; only two *Lythrum salicaria* seedlings and three *Carex crinita* seedlings died after transplanting. These were replaced immediately and their length of growing period adjusted accordingly.

The phytometers were grown in the experiment until 2–10 September, at which time they were harvested. The aboveground portions of the plants were cut off at soil level and bagged. The belowground portions of the plants were harvested by removing soil cores from the ground that were 10 cm in diameter and 20 cm deep. The soil was washed from the belowground structures, which were then bagged separately.

Relative growth rate and competition intensity calculations

Relative growth rate was the dependent variable used to measure the total effect of competition from neighbors on the phytometer. The final biomass of the phytometers was obtained directly and the initial biomass of the phytometers was estimated nondestructively using simple linear regression.

The equation used to calculate relative growth rate is:

$$r = \frac{\ln(b^2/b^1)}{t},$$

where b^1 is the initial biomass of the phytometer (in grams), b^2 is the final biomass of the phytometer (in grams), and t is the growth period (in days). The equations used to calculate total competition intensity and its two components are:

total competition intensity(CI_{TOTAL})

$$= \frac{(r_{NN} - r_{NRS})}{r_{NN}},$$

belowground competition intensity (CI_{BELOW})

$$= \frac{(r_{NN} - r_{NR})}{r_{NN}},$$

aboveground competition intensity (CI_{ABOVE})

$$= \frac{(r_{NR} - r_{NRS})}{r_{NN}},$$

where r_{NN}, r_{NR}, and r_{NRS} are growth rates of the phytometer in the NN, the NR, and the NRS treatments, respectively. All equations include the denominator r_{NN}, which standardizes the measurements to account for different relative growth rates between species and among experimental plots, making them relative measures of competition intensity (Keddy 1989, Campbell and Grime 1992, Grace 1993, 1995, Turkington et al. 1993). The competition intensity equations assume that above- and belowground effects are additive; the implications of this assumption are addressed later in the manuscript. Equations were calculated separately for each indicator species and then averaged to calculate mean competition intensity for each experimental plot. Therefore, each experimental plot yielded one CI_{TOTAL}, one CI_{BELOW}, and one CI_{ABOVE} value for each species and an average CI_{TOTAL}, CI_{BELOW}, and CI_{ABOVE} value based on both wetland plant species. Recent studies have presented both relative and absolute (nonstandardized) measures of competition intensity (Campbell and Grime 1992, Turkington et al. 1993, Reader et al. 1994). In keeping with these studies; mean total, belowground and aboveground competition intensity based on absolute measure were calculated for presentation.

Field measurements

Initial standing crop was measured in a 1-m^2 quadrat in each NN treatment subplot during the experimental setup. The final standing crop was measured in each C treatment subplot at the end of the experiment. These measurements could not be done in the same subplot because they involved the removal of all standing crop biomass. Though there would be some variation in standing crop levels among subplots, study plots were chosen and established in order to minimize between-subplot variation. The rate of production of aboveground biomass in grams per day over the course of the experiment was calculated as:

$$r = \frac{sc^2 - sc^1}{t},$$

where sc^1 is the initial standing crop (in grams), sc^2 is the final standing crop (in grams), and t is the growth period (in days). Litter was collected in a random set of 15 experimental plots in each wetland at the time of harvest. All plant material was dried to constant biomass and weighed.

Light intensity was measured in the same random sample of 15 plots in each wetland using a LI-COR Photosynthetically Active Radiation Sensor. Light measurements were taken 15 cm above the soil (the height of the light meter sensor) and above the vegetation at five locations in each subplot. The height of the second measurement was dependent on the height of the surrounding standing crop, which varied among plots and throughout the growing season. Average vegetation heights in the low and high standing crop wetlands in early summer were ≈10 and 30 cm, respectively, whereas average vegetation heights near the end of the growing season were ≈50 cm and 1.5 m. In the NN, NRS, and the C treatments, light was measured at the four corners of the central 1 m^2 area of the subplot and in the center of the subplot. The nets used in the NR treatments did not permit identical sampling, so measurements were taken on both sides of each phytometer and at three points in the center of the subplot. Light measurements were taken in late June, early August, and early September. Light penetration was calculated as follows:

$$\text{light penetration} = \frac{i_b}{i_a},$$

where i_b is the light intensity near soil level (in microamperes per 1000 μmoles per second per square metre), i_a is the light intensity above the vegetation (in microamperes per 1000 μmoles per second per square metre). The five light penetration values per subplot were averaged to obtain one estimate for the amount of light available to the indicator plants in each experimental subplot at each sampling time.

Soil samples were collected in the same random sample of 15 experimental plots in each wetland and at the same time during the season as the light measurements. Soil samples, ≈3 cm in diameter and 8 cm in depth, were taken from the four corners of the central 1 m^2 of each subplot and at the center of each subplot. The soil samples per subplot were then placed in one bag and thoroughly mixed. Therefore, the experiment yielded one estimate of soil nutrient content per subplot. The soil samples were stored at −15°C in a freezer until March 1993 at which time they were shipped to Agri-food Laboratory in Guelph, Ontario and analyzed for nitrate, phosphorus, potassium, and magnesium content.

Statistical analysis

1. *Prediction of initial biomass of phytometers.*—Simple linear regression was used to predict total biomass of the seedlings used in the experiment. Initial total biomass of the *Lythrum salicaria* seedlings was predicted using the equation logbiomass = 1.11 ± 0.092(logheight) − 1.60 ± 0.11 (F = 149.18, df = 1, 28, P = 0.0001, r^2 = 0.84), and the equation used to predict the initial biomass of *Carex crinita* seedlings was logbiomass = 1.83 ± 0.21(logheight) − 2.91 ± 0.29 (F = 75.54, df = 1, 28, P = 0.0001, r^2 = 0.73). Standard errors for the slopes and intercepts are given.

2. *Competition intensity.*—A two-tailed Student's t test was used to determine if mean total competition intensity was different in the two wetlands. Data from both wetlands were then combined to use a more general and predictive approach to determine whether there was a relationship between standing crop and total competition intensity. Simple linear regression was used to test for an effect of standing crop on total competition intensity. The same analyses were used for above- and belowground competition intensity. All statistical analyses were repeated for each species separately to determine whether the two very different wetland phytometer species yielded similar results. When comparing means, a t test adjusted for unequal variance was used when the assumption of equal variances was not satisfied and the Mann-Whitney U test was used when data were not normally distributed.

3. *Final standing crop, standing crop production and litter.*—Two-tailed Student's t tests were used to determine whether mean final standing crop, mean litter, and the amount of standing crop produced during the experiment were different in the two wetlands.

4. *Light intensity and soil nutrient content.*—Five two-way ANOVAs with repeated measures were used to test for significant effects of wetland site, experimental treatment, and sampling time on light penetration and four soil macronutrient concentrations. SNK, Tukey, and Bonferroni multiple comparisons were performed for significant between-subject main factors at each sampling time and the results were compared to determine which means differed.

5. *Statistical software.*—Statistical analyses were done using SAS 6.04 (SAS 1990) and Sigmastat 1.01 (Jandel 1992).

Results

Total competition intensity and its components

Both mean total competition intensity and mean aboveground competition intensity were different between the low and the high standing crop wetlands; in both cases competition intensity was greater in the high standing crop wetland (Table 1). In contrast, mean belowground competition intensity was not different between the two wetlands (Table 1). Absolute measures of competition intensity are shown in brackets to the right of the relative measures (Table 1). Linear regression showed a strong relationship between total competition intensity and standing crop (F = 31.96, df = 1, 57, P = 0.0001, r^2 = 0.36; Fig. 1a). A significant linear regression was also found between aboveground competition intensity and standing crop (F = 17.69, df = 1, 57, P = 0.0001, r^2 = 0.24; Fig. 1b). There was

TABLE 1. Mean competition intensity in the low and high standing crop wetlands for the two phytometers combined and for each phytometer and the statistical comparison of means.

Competition intensity	Low standing crop wetland mean	High standing crop wetland mean	t	df	P
Average					
Total	0.16 (0.006)*	0.43 (0.015)	−4.93	57	<0.00001
Above	−0.06 (−0.001)	0.21 (0.006)	−3.41	49	0.001
Below	0.19 (0.007)	0.22 (0.009)	−0.56	57	0.58
Carex crinita					
Total	−0.05	0.49	−5.92	41	0.0001
Above	−0.03	0.26	−2.39	42	0.02
Below	−0.02	0.22	−2.22	37	0.03
Lythrum salicaria					
Total	0.38	0.40	−0.38	53	0.71
Above	−0.03	0.17	−2.38	48	0.02
Below†	0.40	0.23	452		0.004

* Values in parentheses correspond to absolute measures of competition intensity.
† Mann-Whitney U test used.

no effect of standing crop on belowground competition intensity ($F = 0.018$, df = 1, 57, $P = 0.89$, $r^2 = 0.0003$; Fig. 1c).

Competition results for each phytometer species

1. *Carex crinita results.*—The two wetlands were significantly different in all three competitive interactions (Table 1). In all cases, mean competition intensity was greater in the high standing crop wetland (Table 1). Simple linear regression analysis detected a significant relationship between standing crop and total competition intensity ($F = 34.76$, df = 1, 53, $P = 0.0001$, $r^2 = 0.40$; Fig. 2a). Similarly, a significant relationship was found between standing crop and aboveground competition intensity ($F = 8.77$, df = 1, 52, $P = 0.005$, $r^2 = 0.14$; Fig. 2b). No significant effect of standing crop on belowground competition intensity was detected ($F = 2.40$, df = 1, 53, $P = 0.13$, $r^2 = 0.044$; Fig. 2c).

2. *Lythrum salicaria results.*—Mean total competition intensity was not significantly different between the two wetlands based on *Lythrum salicaria,* but differences were found for the aboveground and the belowground components of competition (Table 1). The aboveground component was greater in the high standing crop wetland, but the reverse was found for the belowground component (Table 1). A relationship between standing crop and aboveground competition intensity was detected using linear regression ($F = 6.09$, df = 1, 50, $P = 0.017$, $r^2 = 0.11$; Fig. 3b). Simple linear regression analysis failed to detect a significant relationship between standing crop and total competition intensity ($F = 0.78$, df= 1, 53, $P = 0.38$, $r^2 = 0.014$; Fig. 3a). Nor was a significant relationship between standing crop and belowground competition intensity found ($F = 3.79$, df = 1, 50, $P = 0.057$, $r^2 = 0.070$; Fig. 3c).

Field measurements

Mean final standing crop, mean production of standing crop, and mean litter content were all significantly greater in the fertile wetland compared to the infertile shoreline wetland (Table 2).

Light penetration was significantly affected by wetland site, experimental treatment, and sampling time using a repeated-measures analysis of variance (Table 3). Mean light penetration was significantly greater in the low standing crop wetland and significantly greater in the NN and the NR treatments compared to the NRS and the C treatments at all sampling times.

Using repeated-measures ANOVAs, mean [NO_3], [P], [K], and [Mg] were found to be greater in the high standing crop wetland than in the low standing crop wetland at all three sampling times (Table 3). Sampling time significantly affected soil [P], [K], and [Mg]; the former was greatest in early August and the latter two in early September (Table 3). Soil potassium concentration was also significantly affected by experimental treatment. For sampling time 2, mean [K] was significantly greater in the NN treatment than in the NRS and the C treatments, but the mean potassium concentration was not significantly different between the NR treatment and any other treatment (Table 3).

DISCUSSION

General implications

Two views prevail on the role of competition in structuring plant communities along productivity gradients, and they predict different patterns of competition. The patterns emerging from one view are an increase in both the total amount of competition and an increase in both above- and belowground competition as productivity increases. The relative importance of belowground to aboveground competition intensity is therefore constant as productivity increases (e.g.,

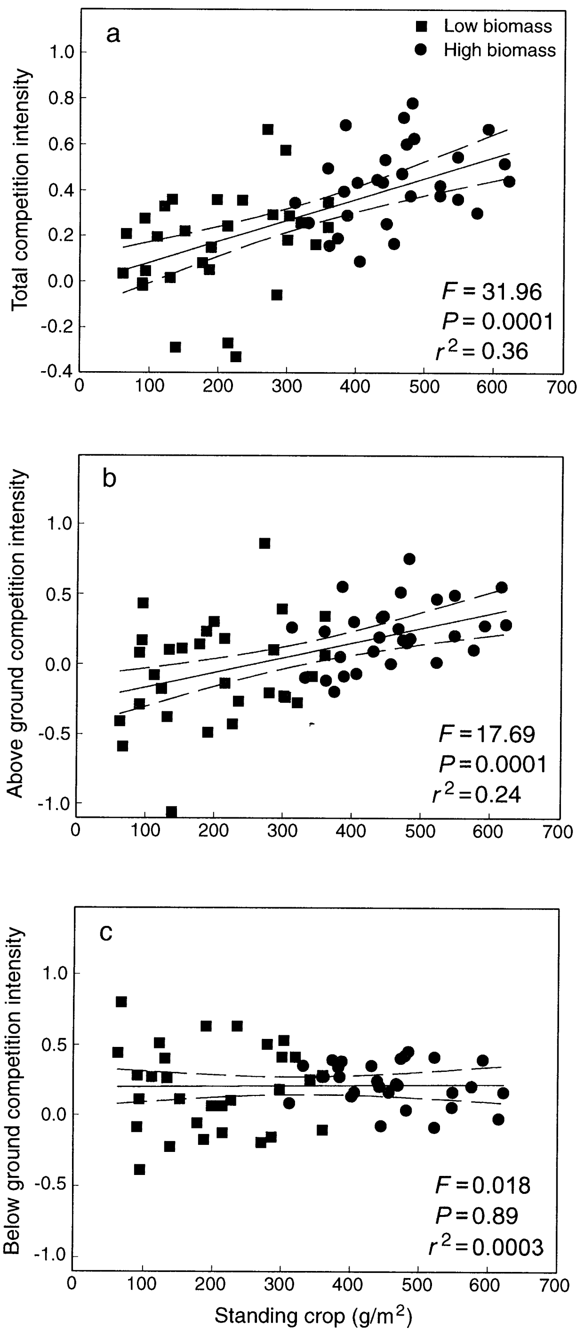

FIG. 1. Relationship between standing crop and (a) total competition intensity (CI) (linear equation: $CI_{TOTAL} = 0.00092 \pm 0.00016$[standing crop] $- 0.0091 \pm 0.059$), (b) aboveground competition intensity (linear equation: $CI_{ABOVE} = 0.0011 \pm 0.00025$[standing crop] $- 0.27 \pm 0.090$) and (c) belowground competition intensity (linear equation: $CI_{BELOW} = 0.000027 \pm 0.00020$[standing crop] $+ 0.20 \pm 0.073$). Standard errors for slopes and intercepts are given. Broken lines give 95% confidence bands and estimates of variance for slopes and y-intercepts are standard errors.

Grime 1973, 1979). These patterns are depicted in Fig. 4a. The general patterns emerging from the second view are an increase in aboveground competition and a decrease in belowground competition as productivity increases, resulting in a decrease in the relative importance of below- to aboveground competition intensity and no net change in the total amount of competition (Tilman 1982, 1987, 1988)(Fig. 4b). Our results suggest that a hybrid of these two alternatives is what actually occurs in wetlands (Fig. 4c). Mean total and aboveground competition intensity increased with standing crop, whereas mean belowground competition intensity remained relatively constant. This resulted in an overall decrease in the relative importance of belowground to aboveground competition intensity; competition was predominantly among roots in the unproductive wetland and was equally partitioned among roots and shoots in the productive wetland (see Table 1 and confidence levels in Fig. 1b, c).

Our study is one of the few field studies designed to test specifically the patterns emerging from current theory using a natural gradient. Related work in old fields and mixed-grass prairie (Wilson and Shay 1990, Wilson and Tilman 1991, 1993) involved artificially created nutrient gradients. Our work does not support either of the two prevalent views in the literature. This suggests that these two main views represent only two alternatives out of many, and reinforces the need for experiments designed to test all possible hypotheses. The issue of whether competition increases with productivity has gone unanswered partly because of debates arising from false dichotomies and partly because of the lack of experimental tests.

Comparison to previous experiments

1. *Total competition intensity.*—Results of this experiment are consistent with the work by Wilson and Keddy (1986) in which diffuse competition (here called competition intensity) was found to increase along an increasing fertility gradient on a lake shoreline. The results are also consistent with the findings of Gurevitch (1986), Reader and Best (1989), and Reader (1990), all of whom found total competition intensity to increase along productivity gradients. In contrast, the results contradict those of Wilson and Tilman (1991,1993) done in old fields, that of Wilson (1993*b*) done in heath and grasslands, and the work by Belcher et al. (*in press*) in alvars, all of which showed no variation in competition intensity along productivity gradients. The results also do not support the findings of Reader et al. (1994) where data from 12 locations across the world were combined to test for an effect of neighbor biomass on total competition intensity. Nor do they support the results of a meta-analysis that found competition intensity was not different in high and low productivity habitats (Gurevitch et al. 1992). It appears no generalizations about total competition intensity are yet possible.

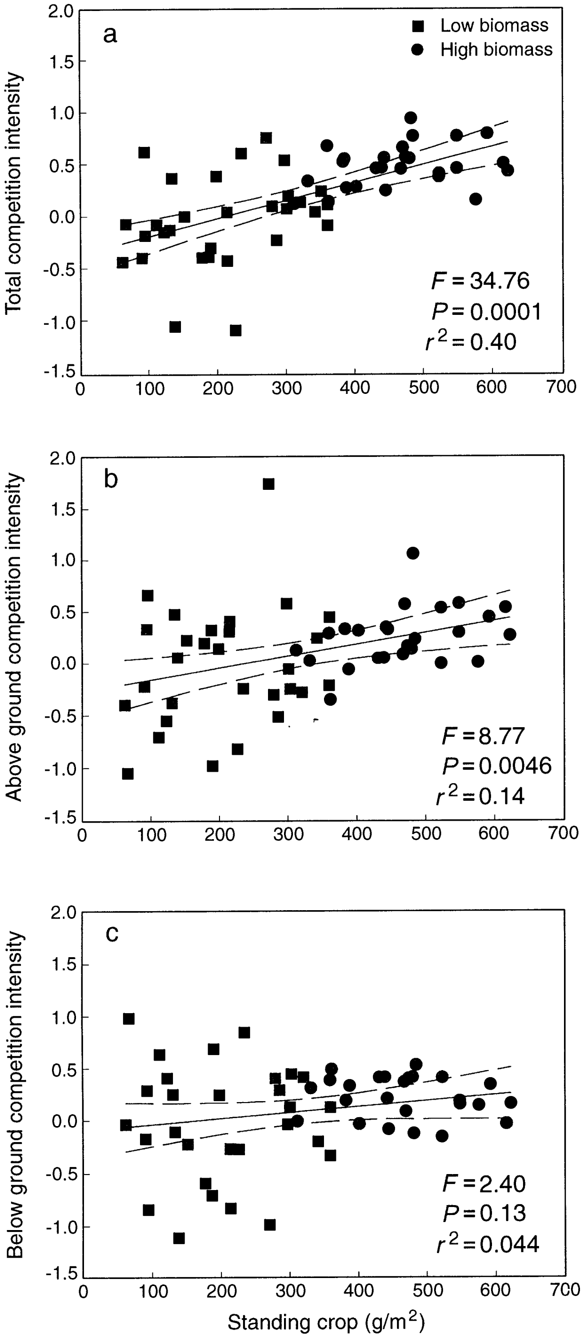

FIG. 2. Relationship between standing crop and (a) mean total competition (CI, competition intensity) (regression equation: $CI_{TOTAL} = 0.0017 \pm 0.00030$[standing crop] $- 0.37 \pm 0.11$, (b) mean aboveground competition intensity (regression equation: $CI_{ABOVE} = 0.0012 \pm 0.00039$[standing crop] $- 0.27 \pm 0.14$, (c) mean belowground competition intensity (regression equation: $CI_{BELOW} = 0.00058 \pm 0.00037$ [standing crop] $- 0.10 \pm 0.14$) using *Carex crinita*. Standard errors for slopes and intercepts are given. Broken lines give 95% confidence bands and estimates of variance for slopes and *y*-intercepts are standard errors.

2. *Aboveground competition intensity.*—In this case, our results are consistent with the work of Wilson and Tilman (1993) who found that aboveground competition intensity in old fields increased with productivity and with the work by Putz and Canham (1992) who found that aboveground competition was more severe in sites with more productive soils. In contrast, Belcher et al. (*in press*) found that aboveground competition intensity was similar in the two halves of a soil depth gradient in alvars, and Wilson (1993*b*) found that aboveground competition intensity was similar in heath and grasslands. Again, no generalizations are yet possible.

3. *Belowground competition intensity.*—Our results are not consistent with any of the five studies that have measured belowground competition intensity. All previous studies found that belowground competition intensity increased as productivity levels decreased (Putz and Canham 1992, Wilson 1993*a, b,* Wilson and Tilman 1993, Belcher et al., *in press*). It appears that wetlands may be fundamentally different from terrestrial sites in terms of belowground competition intensity.

4. *Ratios of belowground to aboveground competition.*—Root competition was predominant in the infertile wetland; in the fertile wetland root competition equaled shoot competition. The results in the infertile wetland are typical of both agricultural pot experiments (Wilson 1988) and experimental field results in old fields (Wilson and Tilman 1991, 1993, Wilson 1993*b*) and shrublands (Putz and Canham 1992). The fact that the relative importance of belowground to aboveground competition intensity changes with productivity suggests that the relative importance of root to shoot competition intensity may indeed depend on the environment (Tilman 1988, Wilson 1988, Putz and Canham 1992). To our knowledge, the intensities of root and shoot competition are statistically different in all other published examples; however the fact that the high standing crop wetland was fertile and wet may explain the inordinate importance of shoot competition in this site. Infertile sandy shorelines are exceptional and unusual wetlands (Moore et al. 1989); most wetlands are more fertile. Therefore the wetland site with higher shoot competition may be typical of the majority of wetlands, even if it is not typical of agricultural experiments and terrestrial habitats.

Choice of phytometer species

Competition intensity varied with the choice of species. Mean total competition intensity based on *Carex crinita* was significantly greater in the high standing crop wetland. When the results for *Lythrum salicaria* were analyzed, mean total competition intensity was greater in the high standing crop wetland but the difference was not significant. As well, total competition intensity increased with standing crop for *Carex crinita* but not for *Lythrum salicaria.* The results for aboveground competition intensity were the same with both

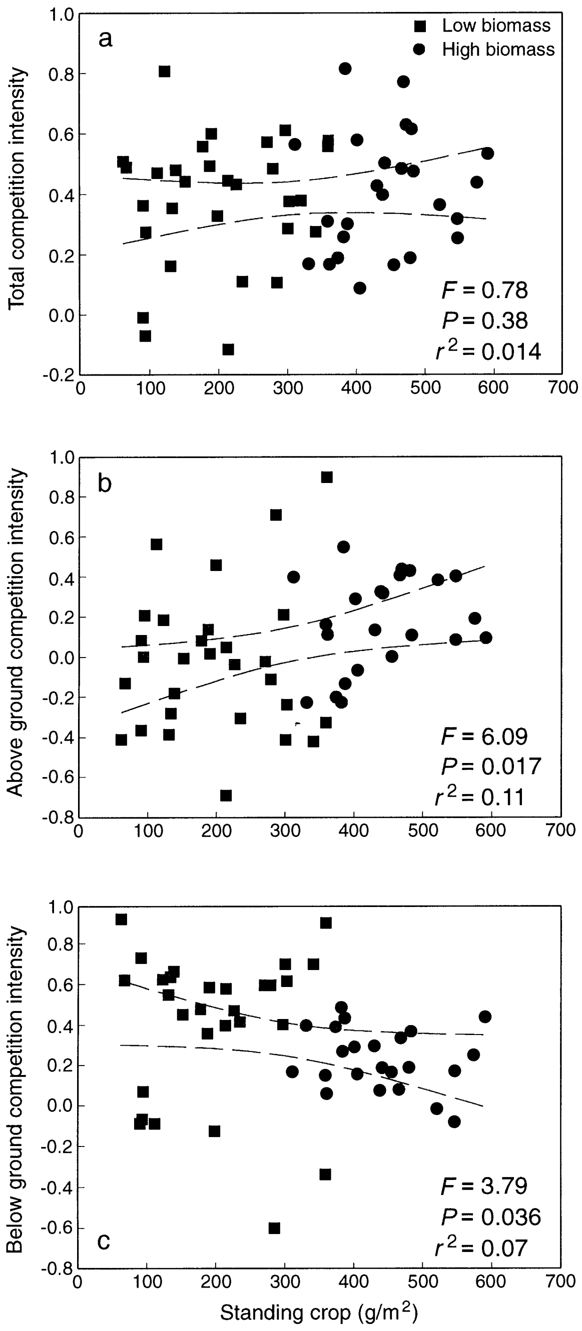

FIG. 3. Relationship between standing crop and (a) total competition intensity (CI) (regression equation: CI_{TOTAL} = 0.00017 ± 0.00019[standing crop] + 0.34 ± 0.065), (b) mean aboveground competition intensity (regression equation: CI_{ABOVE} = 0.00071 ± 0.00029[standing crop] − 0.16 ± 0.098) and (c) mean belowground competition intensity (regression equation: CI_{BELOW} = 0.00055 ± 0.00028[standing crop] + 0.49 ± 0.095) using *Lythrum salicaria*. Standard errors for slopes and intercepts are given. Broken lines give 95% confidence bands and estimates of variance for slopes and *y*-intercepts are standard errors.

of the indicator species—aboveground competition intensity was significantly greater in the high standing crop wetland. The results for belowground competition intensity were quite different. Mean belowground competition intensity based on *Carex crinita* was significantly greater in the high standing crop wetland but the reverse was found for belowground competition intensity based on *Lythrum salicaria.* It should be noted that the probabilities associated with these differences were close to the critical level of 0.05, and linear regression analyses failed to detect a significant relationship between standing crop and belowground competition intensity for either of the indicator species. It is also interesting that the competition intensity measures varied more between species in the low standing crop wetland. As well, *Carex crinita* showed more evidence of overall facilitative effects in the unproductive habitat than did *Lythrum salicaria.*

This study suggests that species vary in their sensitivity to competition occurring in a community, especially to belowground competition, and may vary in the overall type of biotic interaction detected. Furthermore, this difference in sensitivity may be most pronounced in an infertile environment. Therefore, basing competition intensity on the results for more than one species is preferable. Increasing the number of species may lead to a more accurate measurement of competition intensity, but using a large number of species defeats the primary advantage of using phytometer species. The main advantage is the ability to measure the magnitude of competition in a community without measuring the effects on each species. One strategy is to ensure that each guild of plants in the community is represented by one indicator species and that the mean of the results for the indicator species is averaged as was done by Wilson and Keddy (1986).

Considerations for future work

Field studies that have measured competition intensity have used a wide range of biomass levels (Belcher et al., *in press*) and it is thought that the range in biomass level may affect the conclusions (Shipley et al. 1991, Reader et al. 1994, Belcher et al., *in press*). For instance, Reader et al. (1994) did not detect a relationship between competition intensity and standing crop when a standing crop range of 150 g/m^2 was used, but a relationship was found at a site where the range spanned 567 g/m^2. Similarly, a significant relationship was detected in this study where the biomass range was 560 g/m^2. This indicates that standing crop may be a more useful predictor of competition intensity over a wide range of standing crop (Reader et al. 1994). Similar conclusions have been made for the relationship between standing crop and alpha diversity in wetlands (Moore and Keddy 1989). The biomass range is important in interpreting competition intensity results and should be measured and incorporated into any future work in this area of study.

TABLE 2. Mean final standing crop, standing crop produced during the growing season, and litter in the two wetland communities and the comparison of means results.

Variable	Low standing crop wetland mean	High standing crop wetland mean	t	df	P
Final standing crop (g/m^2)	201.27	462.03	−11.42	58	<0.0001
Standing crop produced during the growing season (g·m^{-2}·d^{-1})	1.84	4.08	−9.82	58	<0.001
Litter (g/m^2)	10.44	102.77	−6.47	14	0.0001

Very few experiments have manipulated the availability of light to plants (DiTommasio and Aarrsen 1989). Our experimental design assumes: (1) that the phytometers growing in the NR treatment receive equivalent light to those in the NN treatment and (2) that light penetration through the vegetation canopy is equivalent in the NRS and the C treatments. Table 3 shows that these assumptions are valid. The NR treatment did prevent shading of the indicator plants by surrounding vegetation, and the introduction of the phytometers into the NRS treatment did not measurably affect the light regime of the NRS treatment. As well, light penetration in the NRS and the C treatments was 20–45% less than in the other two treatments, suggesting that phytometers in the NRS treatment were more likely to be limited by light. Thus the use of netting to create a NR treatment appears to be effective and should be considered a feasible field technique for future experimentation.

The netting used in the NR treatment might have increased self-shading and thereby reduced plant growth rates leading to decreased nutrient uptake and a simultaneous increase in both soil nutrients and light availability (Wilson and Tilman 1991). Because soil nutrient concentrations in the four treatments did not differ significantly, it appears that this did not occur. Soil nutrient availability may increase following root death and decomposition. In some cases this has occurred fairly quickly (Eason and Newman 1990) and in other cases it has occurred after 3–4 mo (Seastedt 1988). This experimental design assumed that indicator plants in the NN treatments have greater growth rates due to decreased neighbor effects and not to increased soil nutrient availability following the herbicide application (Aarrsen and Epp 1990). Table 3 shows that no significant differences in soil nutrient concentrations were found among competition treatments and so it appears that any root decomposition in the NN treatment did not increase nutrient levels measurably. Creating NR and NN competition treatments using netting and herbicide does not appear to adversely affect soil nutrient availability and should be considered feasible field techniques for future work.

The experimental design used in this study assumes

TABLE 3. The results of the two-way ANOVAs with repeated measures and multiple comparison of means for mean light penetration, soil [NO_3], [P], [K], and [Mg] measured in four treatments in two wetland communities at three times during the year, 1 (late June), 2 (early August), and 3 (early September).†

	ANOVA				Comparisons‡						
Variable	Factor	F	df	P	Time	Low standing crop	High standing crop	NN	NR	NRS	C
Light	wetland	475.45	1, 112	0.0001	1	0.94^{a}	0.69^{b}	0.94^{a}	0.94^{a}	0.72^{b}	0.63^{b}
	treatment	319.19	3, 112	0.0001	2	0.80^{a}	0.48^{b}	0.88^{a}	0.88^{a}	0.40^{b}	0.39^{b}
	time	170.31	2, 224	0.0001*	3	0.76^{a}	0.44^{b}	0.86^{a}	0.85^{a}	0.37^{b}	0.32^{b}
[NO_3]	wetland	393.84	1, 112	0.0001	1	1.58^{a}	5.79^{b}	3.51	4.02	3.77	3.43
	treatment	0.50	3, 112	0.69	2	1.94^{a}	4.00^{b}	3.22	2.91	2.29	2.81
	time	1.60	2, 224	0.21*	3	1.74^{a}	5.10^{b}	3.50	3.36	3.46	3.37
[P]	wetland	2057.59	1, 97	0.0001	1	1.13^{a}	9.62^{b}	5.50	6.23	6.27	6.39
	treatment	0.67	3, 97	0.57	2	1.53^{a}	9.98^{b}	5.87	6.44	6.58	6.65
	time	16.50	2, 194	0.0001*	3	1.09^{a}	12.43^{b}	6.83	8.00	7.58	8.04
[K]	wetland	633.43	1, 112	0.0001	1	18.03^{a}	49.02^{b}	35.73^{a}	33.90^{a}	32.50^{a}	31.97^{a}
	treatment	2.71	3, 112	0.048	2	17.52^{a}	49.10^{b}	36.67^{a}	34.20^{ba}	31.60^{b}	30.77^{b}
	time	93.46	2, 224	0.0001*	3	21.82^{a}	58.2^{b}	43.07^{a}	40.67^{a}	37.53^{a}	39.37^{a}
[Mg]	wetland	3392.06	1, 112	0.0001	1	27.33^{a}	337.90^{b}	171.43	184.03	180.43	187.57
	treatment	0.54	3, 112	0.65	2	25.48^{a}	362.45^{b}	191.47	200.30	189.87	191.47
	time	25.32	2, 224	0.0001	3	30.92^{a}	374.03^{b}	197.20	213.00	196.10	203.60

* Probability values are Huynh-Feldt Epsilon adjusted because the test for sphericity was rejected.
† ^{a} and ^{b} represent significantly different means.
‡ See *Methods: Experimental design* for explanation of treatment codes.

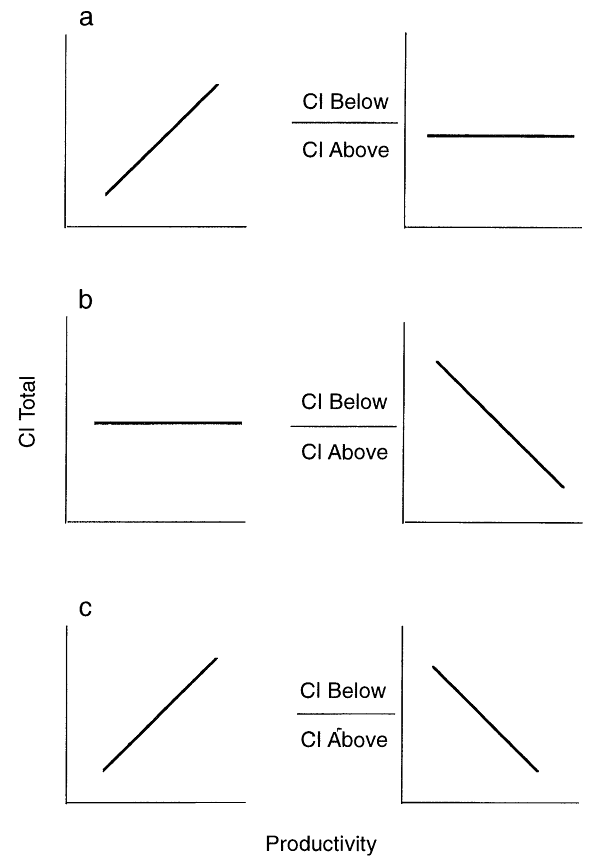

FIG. 4. Three alternative models of total competition intensity (CI) and the ratio of below- to aboveground competition intensity along a gradient of increasing productivity; (a) is associated with Grime (1973, 1979), (b) with Tilman (1982, 1987, 1988), and (c) represents existing data from wetlands (Twolan-Strutt 1994).

that above- and belowground competition intensity are additive and therefore do not interact. Light and nutrient supply are interactive (Grubb 1985), and above- and belowground competition may enhance each other (Clements et al. 1929, Donald 1958, Wilson 1988) or may have different effects (Newman 1981, Wilson 1988). If the components interacted positively in this study, the aboveground competition intensity values would be overestimated. If the components interacted negatively, the values would be underestimated. Our study focused on comparing competition intensity at different levels of standing crop and any such interaction would presumably occur at all levels of standing crop. Interactions between the components of competition were relatively rare in a review of competition pot experiments (Wilson 1988). It is therefore unlikely that the main conclusions of this study are affected by such interactions.

A large number of similarly sized phytometers was needed for this experiment, so seedlings were used instead of adult ramets. The effects of plant dominance are most profound during the seedling stage (Grime 1979), and it is not known whether competition changes after the initial phase of growth of seedlings (Newman 1981). It has also been shown that competition among seedlings and among adults may be different (Shipley et al. 1989). The interactions we observed reflected the amount of competition experienced by seedlings from established neighbor plants, and this should be kept in mind when comparing these results to studies using adult ramets.

This study involved a complex gradient with low standing crop, low fertility, and high light availability at one end and the opposite at the other end. In contrast to artificial nutrient gradients where only soil fertility changes, a natural productivity gradient can vary with respect to fertility and disturbance (Wilson and Keddy 1986, Wilson and Tilman 1993). Although the productivity gradient may be a product of disturbance along the beach, there were no strong disturbances during the experiment. We also attempted to minimize the effects of disturbance by establishing experimental plots in areas where disturbance appeared minimal (i.e., in vegetated areas where the percent cover was not apparently limited by direct removal of plants by ice). Productivity gradients are naturally complex and even though one cannot quantify all factors that change along such a gradient, one is at the very least using a gradient that does occur in nature.

We hypothesize, based on the observations of this study, that in wetlands the total amount of competition increases with productivity. We also predict that the relative importance of belowground to aboveground competition intensity decreases with increasing productivity, primarily due to an increase in aboveground competition. More experimental work is needed to test these predictions.

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