

# Root and shoot competition intensity along a soil depth gradient

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## Summary

**1** Only a handful of studies have measured natural gradients of competition intensity, and only a fraction of these have separated above and below-ground competition. Yet such measurements are essential to distinguish among competing theories and models of plant competition.

**2** We therefore examined the intensity of total, root, and shoot competition along a gradient of soil depth in a herbaceous vegetation system. Above-ground biomass was strongly correlated to soil depth ( $r^2 = 0.65$ ,  $P < 0.001$ ) indicating that as soil resources increased, light decreased along the study gradient. Phytometers (plant indicators) were grown without neighbours, with neighbours' roots only, and with neighbours' roots and shoots. The final biomass of each (after one growing season) was compared in order to determine competition intensity.

**3** Overall, the intensities of total and root competition were significantly greater than zero ( $P < 0.05$ ); that of shoot competition was not. This suggests that competition in this system was primarily below ground.

**4** Competition intensity did not vary significantly along the soil depth gradient.

**5** Results from this and other field studies of competition have produced apparently contradictory results. We suggest a graphical model that relates the various effects of competition and mutualism to biomass levels which may reconcile apparently contradictory field studies.

*Keywords:* alvar, biomass, grassland, resource gradient

*Journal of Ecology* (1995) **83**, 673–682

## Introduction

Environmental gradients are a powerful tool for studying the relationship between competition and environmental factors (Keddy 1991). However, variation in competition intensity, defined as the degree to which a plant is reduced by the presence of neighbours (Weldon & Slauson 1986; Grace 1991; Keddy 1991), has been examined in only a few systems and then with apparently contradictory results. For example, in wetlands (Wilson & Keddy 1986), pastures (Reader & Best 1989; Reader 1990) and grasslands (Gurevitch 1986), competition intensity increases along a gradient of increasing plant biomass and nutrient availability. However, the intensity of competition does not vary predictably with biomass and nutrients in mixed-grass prairie (Wilson & Shay 1990), old fields

(Wilson & Tilman 1991, 1993) and grasslands and old fields across three continents (Reader *et al.* 1994). At the same time, existing models and theories make contrasting predictions about changes in competition intensity along gradients (e.g. Grime 1979; Tilman 1982, 1988; Thompson & Grime 1988; Keddy 1989). One view predicts an increase in both root and shoot competition along a gradient of increasing soil resources and the co-occurring gradient of increasing plant biomass (e.g. Grime 1973, 1979). The opposing view (e.g. Tilman 1985, 1987) says that root competition should decrease and shoot competition should increase along a gradient of increasing soil resources whereas total competition should remain constant (i.e. there is a trade-off for above- and below-ground resources and root and shoot competition are inversely related). The latter model therefore predicts that root competition should predominate where soil resources are limiting. Wilson & Tilman (1991) found that competition is primarily below-ground in less productive sites and is both below- and above-ground

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in more productive sites in old-field vegetation. A more recent study (Wilson & Tilman 1993) found that total competition intensity (below- and above-ground) did not vary with fertility and the intensities of above and below-ground competition were significantly correlated in old fields. The work in old fields was done using artificially created gradients and the use of artificially created vs. natural gradients may affect whether a relationship is found between competition intensity & productivity (Goldberg & Barton 1992). Surprisingly, there have been few studies published that address this question by separating out both the effects of root and shoot competition along a naturally occurring environmental gradient. Root competition has been shown to decrease with increasing soil resources in shrublands (Putz & Canham 1992), forest and prairie (Wilson 1993a) and heath and grassland (Wilson 1993b) and shoot competition has been shown to increase with increasing resources in shrublands (Putz & Canham 1992).

The objectives of our study were to (1) measure the intensity of competition in a vegetation type with shallow soil and low biomass (2) test whether the intensity of competition changed along an environmental gradient and (3) separate the observed effects of above- and below-ground competition.

## Methods

### STUDY SITE

This study was carried out in herbaceous vegetation at the Burnt Lands Alvar near Almonte, Ontario (45°15'N, 76°05'E). This alvar has large areas of open alvar outcrop and meadow; the species composition is described elsewhere (Catling *et al.* 1975; Belcher 1991; Belcher *et al.* 1992).

Alvar is a terrestrial vegetation system growing in thin soil over level limestone rock (Pettersson 1965; Catling *et al.* 1975; Krahulec *et al.* 1986; Bengtsson *et al.* 1988), similar to the cedar glades of mideastern USA (Baskin & Baskin 1985). This system was chosen

because of the strong environmental gradient of soil depth. The gradient ranges from bare limestone outcrop with shallow pockets of soil and sparse vegetation cover, through grassy meadows, to mixed forest where the soil is deepest. This study focused on herbaceous vegetation, occurring on the shallowest portion of this gradient and including a mixture of annuals, perennials, monocots and dicots.

The soil depth gradient also experiences extremes of moisture availability (Catling *et al.* 1975; Baskin & Baskin 1985). In the spring and fall temporary pools of water cover the shallowest soil areas but during mid to late summer moisture becomes limited and drought becomes a problem for the plants in these same locations. Natural disturbances include light grazing by native herbivores (deer, rabbits and insects), occasional fire (now mostly suppressed) (Catling *et al.* 1975) and some frost heaving where autumnal pools cover shallow soil areas (Krahulec *et al.* 1986; Erickson *et al.* 1942).

### THE FIELD EXPERIMENT

The annual *Trichostema brachiatum* (family Labiatae) was used as the phytometer species because it is a common alvar species that occurs naturally over the entire soil depth gradient. Total competition intensity was measured by comparing the final biomass of transplant phytometers (*sensu* Clements & Goldsmith 1924) grown in a no neighbours treatment with treatments having neighbour's roots and shoots (Fig. 1, NN vs. NRS). Root competition intensity was estimated by comparing phytometer biomass in the no neighbours treatment to the treatment with neighbour's roots (Fig. 1, NN vs. NR). Shoot competition was estimated by comparing treatment with neighbour's roots to the neighbour's roots & shoots (Fig. 1, NR vs. NRS).

Competition intensity values were estimated for a total of 56 plots. The plots, each 25 cm × 130 cm, were established in the alvar in May 1989. The vegetation in the study site ranged from sparse vegetation cover on limestone outcrops through to grassy meadows

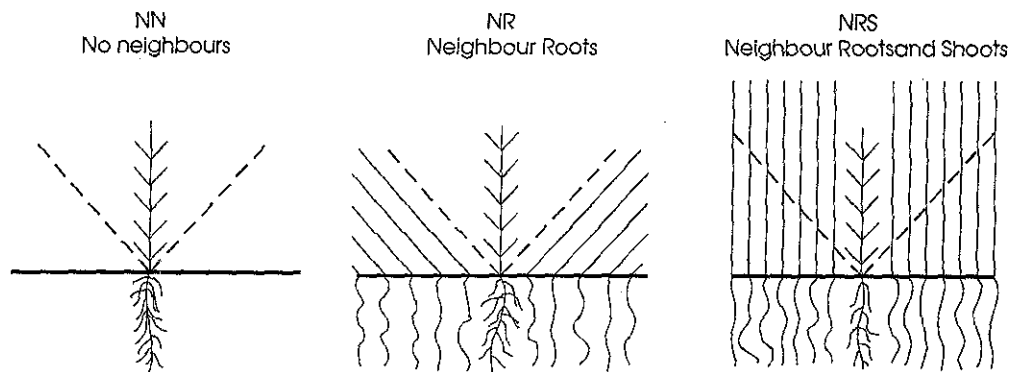


Fig. 1 The experimental design used to measure competition intensity and its above and below ground components (NN: no neighbours; NR: neighbour roots and NRS: neighbour roots and shoots).

dominated by *Sporobolus heterolepis*, so efforts were made to ensure equal sampling along the entire gradient. Each plot was divided into four subplots of 25 cm separated by 10-cm buffer strips. One of the two end-plots was left to be harvested in the fall to measure biomass. The other three subplots were randomly assigned one of the three treatments. A single seedling was transplanted into the centre of each. The three treatments were (Fig. 1):

**1 No neighbours (NN):** vegetation in the subplot was removed with a contact herbicide and the seedling grown without neighbours. The herbicide (Brand name: Round-up) (1.5% solution, 1.5 L of solution per m<sup>2</sup>) was sprayed in the 25-cm × 25-cm subplot on 23 May 1989. As recommended by the herbicide manufacturer, we allowed 10 days for the herbicide to decay in the soil before seedlings were transplanted into treatment plots.

**2 Neighbour roots (NR):** a steel mesh cone (2.5 cm mesh; 13 cm in height; cone hole diameters 2 cm (bottom) and 25 cm (top)) was placed, narrow end down, in the centre of the subplot. Above-ground vegetation was guided to the outside of the cone and the seedling was planted into the centre of the cone. Therefore, the seedling was grown in the presence of neighbour roots and in the absence of neighbour shoots.

**3 Neighbour roots and shoots present (NRS):** the seedling was planted into intact vegetation.

Wire cones were also placed in the NN and NRS treatments to allow for artefact 'cone' effects. These cones were held in place by securing the top rim to a wire frame (25 × 95 × 13 cm tall) which surrounded the three treatment subplots. Throughout the summer, cones were checked weekly and new plant shoots were guided to the appropriate side of the cone. In the NRS treatment the vegetation was allowed to grow up and through the chicken wire and in the NR treatment, vegetation was guided to the outside of the cone.

*Trichostema brachiatum* seedlings at the four leaf stage were transplanted from field populations into the centre of each treatment subplot on 1–2 June 1989. To reduce post-transplant seedling mortality, a 50-cm × 120-cm piece of shade cloth (65% shade) surrounded each plot for the first 2 weeks at a height of 13 cm. During these first two weeks seedlings were watered and 55, 10 and 12 transplants were replaced in the NN, NR and NRS treatments, respectively. The plants were harvested on 27–28 August 1989 when they began to show signs of senescence. Transplants were cut off at ground level using scissors and placed in individual envelopes and above-ground biomass was harvested from each plot. Below-ground biomass was not harvested because it was not possible to distinguish the phytometer roots from the roots of adjacent vegetation. Soil depth was measured at the four corners and centre of each biomass subplot using a 4-mm-diameter pin. Plant material was dried to constant mass in a 60 °C drying oven and weighed.

#### COMPETITION INTENSITY CALCULATIONS

For each site, final transplant biomass was used to calculate three components of competition intensity, total, root and shoot, as follows:

total competition intensity  $CI_T = (P_{NN} - P_{NRS})/P_{NN}$ ,

root competition intensity  $CI_R = (P_{NN} - P_{NR})/P_{NN}$ ,

and shoot competition intensity

$$CI_S = (P_{NR} - P_{NRS})/P_{NN} = CI_T - CI_R$$

where  $P_{NN}$ ,  $P_{NR}$  and  $P_{NRS}$  are the dry weights of the phytometers in the no neighbours, neighbours roots' and neighbours' roots and shoots treatments, respectively. These equations yielded relative measures of competition intensity because  $P_{NN}$  was used to standardize for environmental conditions. A set of equations that excluded the quotient terms were used to calculate the absolute measures of  $CI$ . Both measures of  $CI$  were calculated because the methods may yield different results (Campbell & Grime 1992; Grace 1993; Turkington *et al.* 1993; Reader *et al.*, in press). The competition intensity equations were developed to measure the intensity of negative interactions among plants (i.e. competitive effects) and the values should range from 0 to 1. In addition, these equations can also detect overall positive interactions among plants (i.e. facilitative effects) where the range of competition intensity values is -1 to 0. For the purposes of this study,  $CI$  values greater than 0 are assumed to reflect an overall negative effect of neighbours on transplant performance and  $CI$  values less than 0 reflect a positive effect of neighbours on phytometer performance.

#### STATISTICAL ANALYSIS

To describe the habitat, we examined the relationship between soil depth and biomass using linear regression. In order to determine whether there was an effect of biomass on phytometer survivorship, the survivorship data was divided into two halves and Wilcoxon two-sample tests were used to test the null hypothesis that phytometer survivorship did not differ between the upper and the lower halves of the biomass gradient. A chi-square was used to test the null hypothesis that phytometer survivorship did not differ among the competition treatments. A nonparametric one-way ANOVA was used to test the null hypothesis that final biomass of the phytometers was not different among treatments and the Dunn's multiple comparison test was used to determine which means differed.

We tested for the presence of total competition by asking whether mean  $CI_T$ , over all sites, was significantly different from 0. This was also done for root and shoot competition intensity. We tested for differences among total, root, and shoot competition intensities by using a nonparametric one way ANOVA

and the Dunn's multiple comparison test. Spearman's Rank Correlation coefficients were used to test the hypothesis that competition intensity (total, root and shoot) is related to soil depth and biomass. Non-parametric tests were used because the data did not satisfy assumptions of parametric tests.

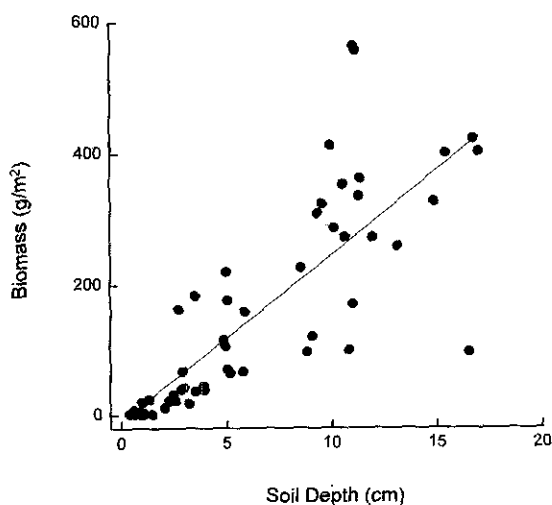
**Results**

**HABITAT DESCRIPTION**

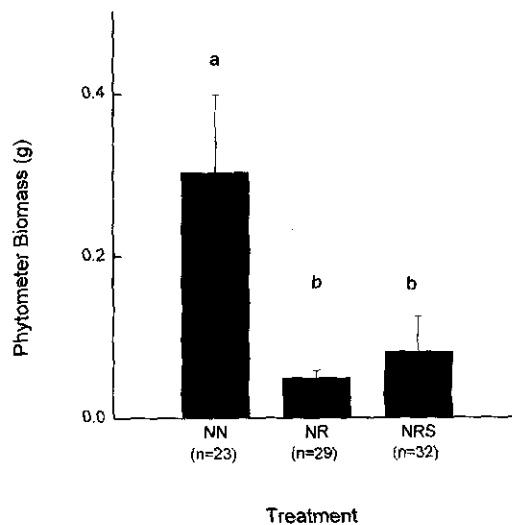
Experimental plots occurred in the soil depth range of 0–17 cm and the biomass range of 0–560 g m<sup>-2</sup>. Standing crop was positively correlated with soil depth ( $r^2 = 0.65$ ,  $P < 0.001$ ; Fig. 2).

**TRANSPLANT PERFORMANCE**

Less than 60% of the transplants survived in each of the competition treatments; 23, 29 and 32 transplants survived out of the 56 transplants in each of the NN, NR and NRS treatments, respectively (see Appendix for raw data). In all treatments, fewer transplants survived in sites located on the lower half of the soil depth/biomass gradient (Wilcoxon two-sample tests,  $P < 0.001$ ) and no transplants survived in sites with less than 1.3 cm deep soil or 21.8 g m<sup>-2</sup> biomass. Survivorship was not significantly different among treatments ( $\chi^2 = 1.5$ ;  $P > 0.05$ ). Final biomass of transplants was significantly different among the three competition treatments ( $P < 0.001$ ). When means were compared, transplant biomass was significantly higher in the no neighbours treatment than in the neighbours roots and the neighbours roots and shoots treatments; the latter two treatment means were not significantly different from each other (Fig. 3).



**Fig. 2** Relationship between above-ground biomass and soil depth within the experimental plots. The relationship is described by the linear equation: biomass = -9.85 + 25.29(soil depth) ( $r^2 = 0.65$ ;  $P < 0.001$ ;  $n = 55$ ).

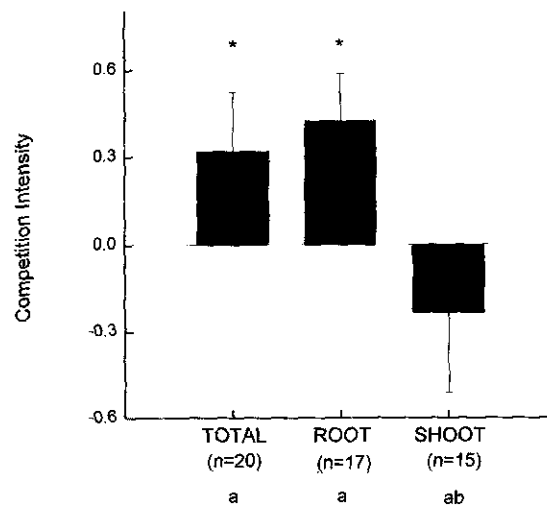


**Fig. 3** Mean biomass of transplant phytometers in each competition treatment (NN, no neighbours; NR, neighbour roots; NRS, neighbour roots and shoots). Bars indicate + 1 SE (sample sizes are shown in brackets below). Means sharing the same letter are not significantly different ( $P > 0.05$ ).

**COMPETITION INTENSITY**

Due to the mortality, all three components of competition could not be calculated in all experimental sites and the sample sizes were reduced ( $CI_T$ :  $n = 20$ ,  $CI_R$ :  $n = 17$ ,  $CI_S$ :  $n = 15$ , see equations above). The sample sizes of the competition measures were unequal because the equations used to calculate them involve the biomass of phytometers grown in different treatments. Similar patterns of results were obtained with absolute and relative measures of competition intensity, so the results will be presented for relative competition intensity data only.

Total competition intensity was significantly greater than zero ( $P < 0.05$ ; Fig. 4) but there were no



**Fig. 4** Mean competition intensity for total, root and shoot competition. Bars indicate + 1 SE (sample sizes are shown in brackets below). Asterisk (\*) indicates that competition intensity was greater than 0 ( $P < 0.05$ ). Means sharing the same letter are not significantly different (Wilcoxon signed ranks test,  $P > 0.05$ ).

significant relationships between total competition intensity and either soil depth or biomass (Fig. 5a).

Total intensity can be split into above ground and below ground components. Root competition intensity was significantly greater than zero ( $P < 0.05$ ), whereas shoot competition intensity was not (Fig. 4). Both root or shoot competition intensity were not significantly correlated with soil depth or biomass (Fig. 5b and c respectively).

## Discussion

### COMPETITION INTENSITY IN ALVAR VEGETATION

Lugo & McCormick (1981) assign a high stress index to shallow soil communities. The high mortality in this experiment, especially where soil was shallowest, tends to confirm that environmental stress was high. Yet, in spite of the stressful conditions, competition was still detectable. This is consistent with other experimental studies of shallow soils (Sharitz & McCormick 1973). Fowler (1986) has also argued that competition is not uncommon in arid systems.

The mean competition intensity value for shoots was negative (Fig. 4), suggesting that facilitation occurred. Both Wilson & Keddy (1986) and Twolan-Strutt (1994) found similar evidence for facilitation in low biomass sites along shoreline gradients. In addition, we found that transplant survivorship was higher in the 'with-neighbour' treatments (10% higher in the NR treatment and 15% higher in the NRS treatment, though the difference was not significant). At the alvar, limestone is often exposed and the temperature at ground level can be very high (Stephenson & Herendeen 1986). Perhaps neighbour shoots reduce heat stress and evaporation of the already limited water by providing some shade (Bradshaw & Goldberg 1989). Neighbour roots may also be beneficial by providing mycorrhizae (Grime *et al.* 1987) although Eissenstat & Newman (1990) found that mycorrhizae do not alter the competitive balance. There has been extensive discussion over competition and a growing number of competition field experiments; in contrast possibilities for mutualism as a key interaction are generally overlooked (Boucher *et al.* 1982; Keddy 1989). Future studies should specifically include tests for the presence of facilitation.

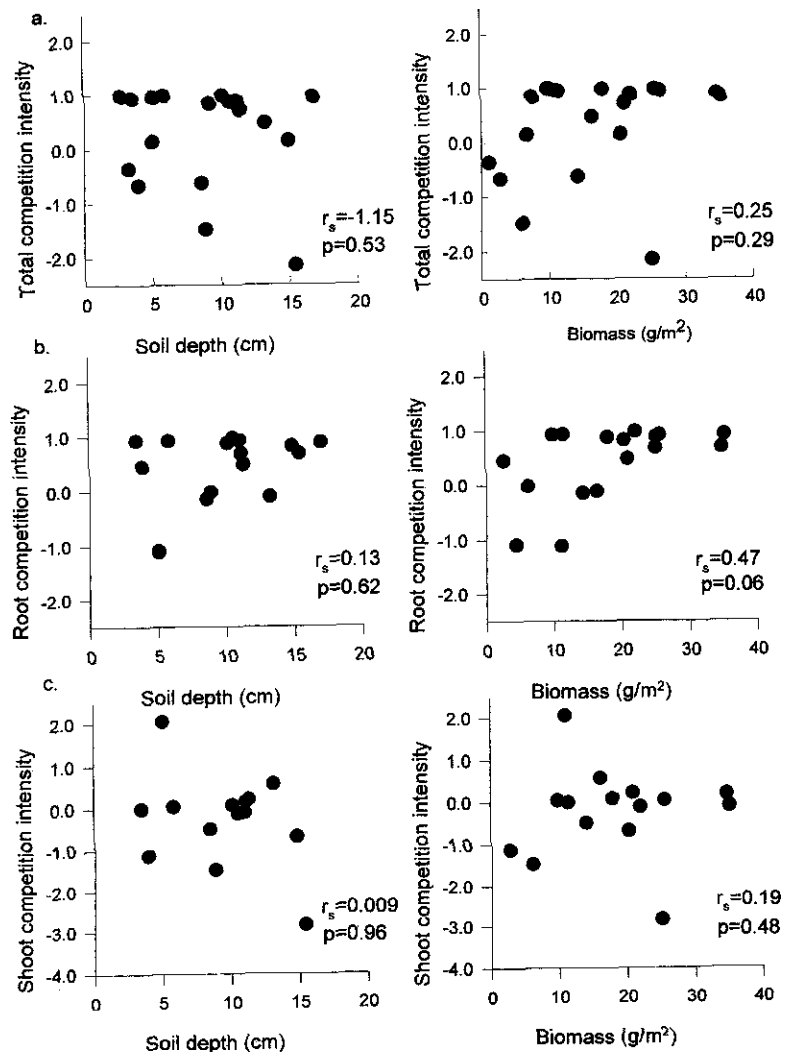


Fig. 5 Total (a), root (b) and shoot (c) competition intensity plotted against both soil depth and biomass.

The method used in this experiment allowed us to examine the intensity of root and shoot competition separately, and we found that only root competition was significant. This is consistent with what we might expect from a consideration of mechanism. In our low biomass site there was minimal shade and thus shoot competition should be unimportant. We found, as expected from this line of reasoning, that competition for soil resources predominated. Similarly, in a fertilized grassland, Wilson & Tilman (1991) found that root competition was most important in lower biomass sites but that competition shifted to both above- and below-ground where fertility and biomass were higher. Both sets of results support the contention that in sites where soil resources are limited, competition should be below-ground. Tilman's model also predicts an increase in shoot competition and a decrease in root competition along a gradient of increasing productivity. An inverse relationship between root and shoot competition was found by Wilson & Tilman (1993) but our results do not support this simple trade-off. No significant relationships were found either between the components of competition and soil depth or between the components of competition and biomass.

#### COMMENTS ON METHODS

Due to high mortality rates, our final sample sizes were low. Low sample sizes, combined with less powerful nonparametric correlation analysis, may have reduced the likelihood of detecting significant correlations. Furthermore, our study involved just one phytometer species. In some studies, measures of the intensity and importance of competition have been shown to be species-dependent (DiTommasio & Aarssen 1989; Putz & Canham 1992; Reader & Bonser 1993; Wilson 1993b). In spite of these two points, we do have clear results for a common alvar species that occurs naturally across the entire gradient. Further studies should include the use of several phytometer species and the result averaged, as was done in Wilson & Keddy (1986).

The design assumes no interaction between above- and below-ground competition. We do not believe this to be true, but we assume that the main effects are large enough to minimize this interaction effect. If an interaction were important it could mean that by releasing the phytometers from shading by neighbours in the NR treatment, we improved their below ground competitive ability, thereby leading to an underestimate of the intensity of below-ground competition. In addition, the NR treatment removes the shading of the phytometer, but still shades the soil surface, thereby leaving in possible commensalistic effects on the phytometer. This in turn could lead to an underestimate of the intensity of below-ground competition. Both of these effects (possible interactions, the benefits of shading the soil) mean that

actual below-ground competition may be greater than our values. Similarly, since shoot competition intensity was obtained by subtraction, we may have therefore overestimated it. If the two components interacted with each other in this manner, the differences between root and shoot competition intensity would be greater.

Using herbicide to kill plants may have left rotting roots that lead to greater phytometer growth in the NN treatment, thereby overestimating the difference between the cleared NN plots and the uncleared NRS plots, which in turn would lead to overestimates of total competition intensity. Roots have been shown to decompose quickly (Eason & Newman 1990) and to decompose only after 3–4 months (Seastedt 1988). However, both the above- and below-ground calculations used the NN plot for comparison, so this effect should not have influenced the estimates of above vs. below ground effects.

It should also be pointed out that most of the plants that required replacement within the first 2 weeks of the experiment were those of the NN treatment. Therefore, most phytometers growing in this treatment grew for 1–2 weeks less than most of those in the other treatments. This could have decreased the difference between the final biomass of plants in the NR and NRS treatments compared to those of the NN treatment; leading to underestimates of total competition intensity.

There are currently at least three ways to measure competition intensity in a plant community: relative (e.g. Wilson & Keddy 1986), absolute (e.g. Campbell & Grime 1992) and per gram (e.g. Goldberg & Werner 1983). We have used the first two to measure the total effects of neighbours on our phytometers and expressed them on a relative and an absolute per plant basis. Both yielded the same results, and we presented only the former. We suspect that some of the acrimonious debate on competition gradients and on size-related competitive ability arises because some workers think exclusively on effects per unit of biomass and others on a per-plant basis.

Finally, we have based our final biomass values on phytometer shoots only because root biomass could not be harvested. Therefore, any variation in the ratio of root to shoot biomass along the gradient are not reflected in our measures of biomass and could subtly alter our findings. However, there was more than one order of magnitude difference among phytometer sizes, and mean control values were more than four times the treatment values. At this scale of variation we could expect root and shoot biomass to be highly positively correlated. We cannot say how changes in root and shoot values would have modified our results.

#### RESOURCE GRADIENTS

Gradients are an important research tool in ecology (Whittaker 1967; Pielou 1977; Keddy 1991). In this

study we specifically chose a system with a striking gradient: soil depth. Both nutrient and moisture availability should be proportional to the cube of the soil depth. Figure 2 shows the importance of this gradient in alvars – 65% of the variation in vegetation biomass can be predicted from soil depth. Yet, in spite of this, no evidence for a gradient of competition intensity was found. There was no correlation between competition intensity and biomass or soil depth using either absolute or relative competition measures. Other study systems where this relationship is not evident include marsh (Shipley 1987), fire-disturbed prairie (Wilson & Shay 1990) and fertilized old fields (Wilson & Tilman 1991, 1993). However, competition intensity does vary along a resource/biomass gradient in other situations such as rock outcrop (Sharitz & McCormick 1973), shoreline (Wilson & Keddy 1986), arid grassland (Gurevitch 1986), and abandoned pasture (Reader & Best 1989; Reader 1990).

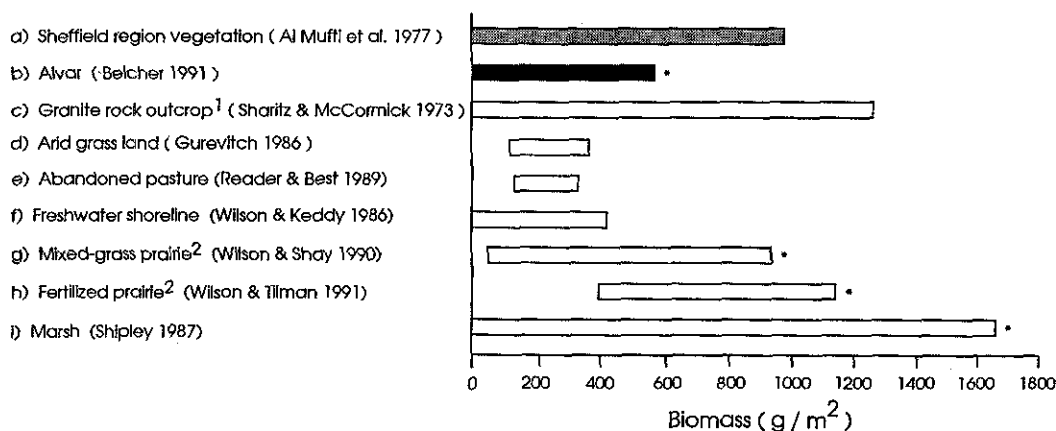
Important differences between these studies and systems may account for their contradictory results. First, consider the type of gradient. These examples include both natural and experimental variations in resources and/or disturbance (see Fig. 6). Second is the choice of response variable and phytometer. While some studies use biomass or growth of an indicator plant to measure competition intensity (this study, Wilson & Keddy 1986; Wilson & Shay 1990; Shipley *et al.* 1991; Wilson & Tilman 1991, 1993) others use population attributes such as recruitment, survival and population growth (Gurevitch 1986; Reader & Best 1989; Reader 1990). Different plant traits may be affected by different time scales and, perhaps, biomass levels. Third, and probably most important, is the level and extent of the biomass range considered in these studies (Fig. 6). Our experiment included a biomass range of 0–560 g m<sup>-2</sup> (Fig. 2). Compared to other studies we were working in the low to mid-range of the overall biomass gradient illustrated. Recent

work by Reader *et al.* (1994) showed that competition intensity did not vary with biomass in eight of nine study sites; interestingly, the exception was the one with the greatest range in biomass (approximately 100–600 g m<sup>-2</sup>). To make more direct comparisons among these published studies, one must consider differences such as type of gradient, response variable, and extent of gradient among studies.

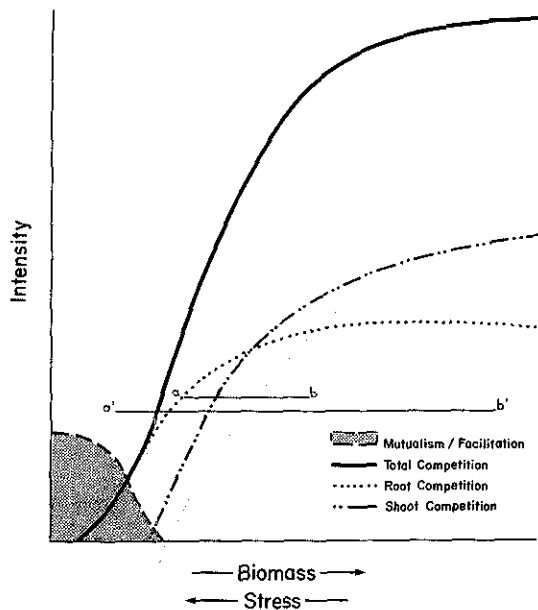
Figure 7 presents one way which might reconcile some conflicting results. In this model, total competition intensity increases along a gradient of biomass and reaches a plateau at some level, the maximum competition intensity for the system. At extremely low biomass levels, competition may be unimportant and in such situations the effect of facilitation or mutualism (e.g. shading and mycorrhizal associations) is probably more significant. Moving up the biomass gradient, the effect of facilitation decreases while the effect of competition increases. At this point, where biomass levels are still too low for shading to occur, shoot competition is not important and it is root competition that has an effect. Continuing up the gradient, the intensity of root competition increases but its effect becomes relatively unimportant as light becomes the main limiting factor and the effect of shoot competition is increasingly evident.

In this study there was some evidence for facilitation, especially at the low end of the soil depth/biomass gradient. The effect of competition was measurable and primarily due to root competition. In a higher biomass grassland (450–1150 g m<sup>-2</sup>; Fig. 6, Wilson & Tilman 1991) competition at the lowest end of the gradient is below ground and at the upper end is both below and above ground.

Those studies which have found competition intensity gradients have emphasized the lower ranges of biomass such as are found in arid grassland (Gurevitch 1986) and abandoned pasture (Reader & Best



**Fig. 6** The range of above-ground biomass over which competition was examined in a number of community types. Competition was not measured in (a) stippled, but this study is included since it illustrates the biomass range relevant to Grime's theory (1979) predicting variation in competition along biomass gradients. The black bar (b) represents the community used in this study. (1, competition measured in simulated rock outcrop conditions. 2, experimentally created as opposed to naturally occurring gradients). \*, no variation in competition intensity with biomass reported).



**Fig. 7** Hypothesized changes in the intensity of mutualism and competition along a gradient of decreasing stress. There are two important parts to this figure. (1) Mutualism and facilitation occur in low biomass sites, competition occurs in the higher biomass sites. (2) A study along a short gradient within a site of modest productivity (*a-b*) would detect major changes in the relative importance of root and shoot competition. In contrast, a study along a natural gradient (*a'-b'*) would find that the intensity of root and shoot competition is positively correlated, as both would go from being negligible to being important. Thus, depending upon the scale, one could either emphasize changes in resource ratios, or increases in competition intensity above and below ground.

1989; Reader 1990). In contrast, those previously published studies which have not found such gradients, such as freshwater marsh (Shipley *et al.* 1991) or fertilized old fields (Wilson & Tilman 1991, 1993), had higher biomass ranges. This is consistent with Fig. 7 where the greatest changes in competition intensity occur in the low to middle biomass levels (200–600 g m<sup>-2</sup> range), and an asymptote is approached at higher levels (approaching the 1000 g m<sup>-2</sup> range.)

Figure 7 does not, however, account for all the differences among studies, nor can it reasonably be expected to. There are many causes of biomass gradients and it may be that some causes, such as resource gradients, do not change competition intensity (Shipley *et al.* 1991; Wilson & Tilman 1991, 1993). Furthermore, the ranges of Fig. 6 do not show which regions predominated in the study cited (i.e. they do not necessarily emphasize the most important part of the biomass gradient). For example, Shipley *et al.* (1991) are shown covering the entire range, but the sites were predominantly in the 400–1000 g m<sup>-2</sup> range.

Two studies conducted in wetlands yielded apparently different results. Wilson & Keddy (1986) found a competition intensity gradient whereas Shipley *et al.* (1991) did not. Thus these studies appear contradictory. However, Shipley *et al.* (1991) developed a nonlinear regression equation ( $CI_T = -0.20 +$

$0.13B^{0.5}$ , where  $CI_T$  is total competition intensity and  $B$  is biomass) from the data in Wilson & Keddy (1986) and show that it predicts the results of the data in Shipley *et al.* (1991). This is important for two reasons. First, it shows that the competition intensity/biomass relationship can be extended from one study site to another. Secondly, it is based upon a model assuming a nonlinear relationship between competition intensity and biomass. Shipley *et al.* (1991) specifically note that this model predicts relatively small changes in competition intensity over ranges they used.

We include Fig. 7 for three reasons. First, it emphasizes the importance of specifying both the range of biomass values used and their frequency distribution. Secondly, it offers a possible reconciliation between studies finding evidence of both for and against trade-offs in root and shoot competition. Lastly, it is consistent with existing studies in that those emphasizing higher biomass ranges have tended not to find competition gradients. Further field experiments are needed.

### Acknowledgements

We thank Elizabeth Belcher, Harold Lee and Kristin Nielsen for field assistance, and Jacques Helie and Evan Weiher for help with preparing the manuscript. We thank Deborah Goldberg, Roy Turkington and Scott Wilson and several anonymous referees for helpful comments on earlier versions of the manuscript. This work was supported by an Ontario Graduate Scholarship to J. Belcher and a NSERC grant to P. Keddy.

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Received 7 July 1993

revised version accepted 25 August 1994

## Appendix

Raw data. The soil depth, plot biomass and density, and raw biomass of the phytometers in each of the three treatments (NN, no neighbours; NR, neighbour roots; NRS, neighbour roots and shoots). Phytometers which did not survive and missing data are indicated by dashes. (From appendixes 3.4 and 3.5 in Belcher 1991.)

Sample	Soil depth (cm)	Plot biomass (g 0.0625 m <sup>-2</sup> )	Plot density (g m <sup>-2</sup> )	Phytometer biomass (g)		
				NN	NR	NRS
1	10.82	6.18	98.9	–	–	0.0701
2	8.82	6.04	96.6	0.0438	0.0444	0.1085
3	9.10	7.54	121.0	0.1858	–	0.0302
4	4.94	6.64	106.0	0.0704	–	0.0603
5	4.88	7.21	115.0	–	0.0249	0.0274
6	0.40	0.16	2.6	–	–	–
7	1.00	1.24	19.8	–	–	–
8	1.34	1.52	24.3	–	0.0859	–
9	0.86	0.25	4.0	–	–	–
10	2.98	2.58	41.3	–	0.0889	0.0481
11	5.76	4.11	65.8	–	0.0657	0.0487
12	5.02	4.37	69.9	0.0157	0.0327	–
13	2.30	1.36	21.8	–	0.0562	–
14	3.22	1.10	17.6	0.1570	–	0.2125
15	5.16	4.01	64.2	–	0.1012	0.0891
16	3.92	2.75	44.0	0.0481	0.0260	0.0799
17	3.54	2.27	36.3	–	–	–
18	3.96	2.42	38.7	–	–	–
19	1.46	0.11	1.8	–	–	–
20	0.92	0.09	1.0	–	–	–
21	2.88	2.51	40.2	–	0.0533	0.0740
22	2.50	1.95	31.2	–	–	–
23	2.58	1.41	22.6	–	–	–
24	1.06	0.23	3.7	–	–	–
25	0.60	0.46	7.4	–	–	–
26	0.88	0.33	5.3	–	–	–
27	0.96	0.05	0.8	–	–	–
28	10.14	17.98	287.7	1.0782	0.1208	0.0242
29	10.64	17.10	273.6	–	0.0671	0.0367
30	8.52	14.16	226.6	0.0447	0.0511	0.0727
31	2.06	0.68	11.0	–	–	–
32	1.08	0.16	2.6	–	–	–
33	0.62	0.07	1.0	–	–	–
34	17.00	25.12	401.9	0.0821	0.0091	–
35	11.14	34.78	556.5	0.0948	0.0293	0.0118
36	11.02	10.63	170.1	–	–	–
37	9.32	19.33	309.3	–	–	–
38	2.72	10.19	163.0	1.2135	–	0.0188
39	2.90	4.19	67.0	–	–	0.0128
40	4.98	13.78	220.5	–	–	0.2324
41	5.84	9.90	158	1.7190	0.1155	0.0228
42	5.04	11.04	176.6	0.6086	1.2824	0.0272
43	3.50	11.47	183.5	0.7744	0.0464	0.0450
44	14.88	20.41	326.6	0.0535	0.0094	0.0458
45	–	25.60	409.6	0.1348	0.0105	0.0041
46	9.56	20.20	323.2	–	0.0099	0.0191
47	13.14	16.22	259.5	0.0074	0.0082	0.0039
48	11.38	22.61	361.8	–	0.0128	0.0137
49	11.04	35.20	563.2	0.0724	0.0052	0.0122
50	9.96	25.75	412.0	0.2394	–	–
51	10.54	22.05	352.8	0.1711	0.0027	0.0214
52	11.32	20.95	335.2	0.0259	0.0133	0.0075
53	16.76	26.38	422.1	0.0843	–	0.0054
54	11.94	17.07	273.1	–	0.0098	–
55	15.42	25.03	400.5	0.0324	0.0101	0.1019
56	16.54	6.00	96.0	–	0.0054	0.0095