Effect of Nutrient Level on Competition Intensity in the Field for Three Coexisting Grass Species

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Effect of nutrient level on competition intensity in the field for three coexisting grass species

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Abstract. A field experiment encompassing both neighbour- and nutrient-manipulations was conducted in a nutrient-im-poverished old-field habitat to investigate how the intensity of plant competition was affected by soil nutrient level. Three perennial grasses were used as target species: Agropyron repens, Poa pratensis and Phleum pratense. Neighbour manipulations involved the removal (through herbicide application) of all neighbouring vegetation within a 20 cm or 40 cm radius around target plants. Target performance was measured under five levels of added nutrients (N-P-K) in both the neighbour-removal plots and in non-removal (control) plots. Both neighbour and nutrient manipulations had a highly significant effect on both biomass and tiller production but the interaction between these treatments was generally insignificant. Below-ground/above-ground biomass quotient was affected only by neighbour manipulations and was greatest in the control plots (with no neighbours removed) for all three species. The suppressive effect of neighbours was not marked-ly affected by nutrient level. However, yield suppression showed a significant decreasing trend with increasing nutrient level for biomass production in Agropyron and an increasing trend for tiller production in Phleum. For Poa, there was no trend in the intensity of competition across nutrient level. The results suggest that the general intensity of competition within this community neither increases nor decreases with increasing nutrient level. Rather, coexisting species appear to respond individually in terms of the intensity of competition that they experience. These results conflict with predictions from the triangular C-S-R model of plant strategies. However, they are consistent with a recently modified ‘habitat template’ model for vegetation.

Introduction

According to traditional r/K selection theory (MacArthur & Wilson 1967) the intensity of competition generally decreases as disturbance or predation intensity increases (Harper 1977). For vegetation, this prediction is derived mainly from the assumption that, because such factors commonly limit plant biomass production, they will also limit the demands made on available resources and thus limit the opportunities for neighbouring plants to deny resources to each other (Weaver & Clements 1938; Taylor, Aarssen & Loehle 1990). This prediction has remained widely accepted, although there is surprisingly little empirical data to support it. Wilson & Keddy (1986) showed that competition intensity in shoreline plant communities generally decreased with decreasing standing crop or soil organic content which were negatively correlated with increasing disturbance from exposure to waves (see also Keddy 1989).

The effect of resource impoverishment level (habitat fertility) on competition intensity in vegetation is much more controversial. There are three main theoretical predictions. The first and most traditional view is that competition intensity should be greater when resources are in shorter supply. In reviewing the literature, Wilson (1988) noted that, “It has often been suggested (Brenchley 1922; Nedrow 1937; Welbank 1961; Bandeen & Buchholtz 1967) that if two species compete for a given resource, e.g. water or nutrients, addition of that resource will reduce its deficiency and so reduce the intensity of competition” (p. 290). The second prediction is derived from the more recent C-S-R theory of plant strategies (Grime 1973; 1979) which extends r/K theory by recognizing a third major selection factor associated with the level of stress. According to Grime (1988, p. 382), the “ultimate determinants of the stress-tolerant strategy in plants” relate to “low availability of
mineral nutrients”. C-S-R theory predicts that competition intensity within vegetation should generally increase not only as disturbance level decreases, but also as habitat fertility increases. “The essential feature of this emerging view of competition is that it is a process which reaches its maximum intensity in environments where there is an abundance of resources” (Grime & Hodgson 1987, p. 287).

This latter prediction from C-S-R theory has generated considerable controversy (Newman 1973; Pigott 1980; Aarssen 1984; Chapin & Shaver 1985; Grubb 1985; Welden & Slauson 1986; Tilman 1987, 1988; Thompson & Grime 1988; Taylor, Aarssen & Loehle 1990). Surprisingly however, there have been few attempts to test it empirically within natural vegetation. Some recent studies appear to support the ‘C-S-R’ prediction that competition intensity generally increases with increasing habitat fertility (Gurevitch 1986; Reader & Best 1989). Other studies however, have failed to support it (Rahman 1976; Welden, Slauson & Ward 1988; McGraw & Chapin 1989; Tilman & Cowan 1989) and are consistent with the third prediction, i.e. that general competition intensity within vegetation is unaffected by habitat fertility. According to this view, competition intensity is determined primarily by the resource supply/demand ratio and this ratio does not vary in any predictable way across a habitat fertility gradient (Taylor, Aarssen & Loehle 1990). This view can also be traced back to the early literature on plant competition; “competition always occurs when two or more plants make demands for light, nutrients, or water in excess of the supply. If there is enough of any one of these factors, such as water in a swamp, there is no competition for that factor” (Weaver & Clements 1938, p. 148).

In this study, we used a combination of neighbour removal and nutrient addition within natural vegetation to investigate the effects of soil nutrient level on the intensity of competition for three perennial grasses under a constant level of disturbance. The use of such field experiments in natural vegetation has increased dramatically within the last two decades (DiTommaso & Aarssen 1989; Aarssen & Epp 1990) but few studies (e.g. Whigham 1984) have employed both types of manipulation together in the same experiment. The advantage of this approach is that it allows simultaneous control of both the effects of competitors and the ‘objects’ of competition (i.e. nutrients) themselves. Analysis of the interaction between these treatment effects thus provides a direct and powerful test of the above predictions especially when several coexisting species are examined simultaneously.

### Table 1. Percent cover of the common species in the study field during mid July 1987 using the point-intercept method within 40 randomly spaced 1 m × 1 m quadrats. (Species with cover values below 1% are not listed.)

<table>
<thead>
<tr>
<th>Species</th>
<th>Percent cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solidago canadensis</td>
<td>31.8</td>
</tr>
<tr>
<td>Potentilla argentea</td>
<td>24.7</td>
</tr>
<tr>
<td>Agropyron repens</td>
<td>24.5</td>
</tr>
<tr>
<td>Poa pratensis</td>
<td>24.3</td>
</tr>
<tr>
<td>Phleum pratense</td>
<td>14.5</td>
</tr>
<tr>
<td>Agrostis stolonifera</td>
<td>8.3</td>
</tr>
<tr>
<td>Vicia cracca</td>
<td>7.3</td>
</tr>
<tr>
<td>Poa compressa</td>
<td>7.0</td>
</tr>
<tr>
<td>Aster spp.</td>
<td>3.2</td>
</tr>
<tr>
<td>Medicago lupulina</td>
<td>2.6</td>
</tr>
<tr>
<td>Trifolium pratense</td>
<td>1.8</td>
</tr>
<tr>
<td>Chrysanthemum leucanthemum</td>
<td>1.8</td>
</tr>
<tr>
<td>Cirsium vulgare</td>
<td>1.0</td>
</tr>
<tr>
<td>Potentilla recta</td>
<td>1.0</td>
</tr>
</tbody>
</table>

1 Nomenclature follows Gleason & Cronquist (1963)

### Materials and Methods

#### Field site

The experiment was conducted in 1987 in an old-field located near Harrowsmith, Ontario, Canada (44° 25'N, 76° 39'W). The field is ca. 2 ha in size and is separated from adjacent hayfields by fencing and hedgerow. The site is relatively flat with shallow sandy loam topsoil (10 cm mean depth) over limestone bedrock. The site was chosen because of its chronic nutrient-impoverishment; available nitrate and phosphorus concentrations averaged 6 and 3 ppm respectively based on a preliminary soil analysis. This made it possible to establish an experimental nutrient gradient in the field by adding nutrients to the soil in different amounts.

In 1970, the field had been tilled and sown with a 50:50 mixture of *Phleum pratense* and *Trifolium pratense* (J. Foster pers. comm.) and was mown annually for hay until 1979. Between 1979 and the time of the present study, the field had been abandoned. The site is dominated by several perennial dicots and graminoids (Table 1) characteristic of many secondary successional fields in eastern Canada.

#### Selection and handling of target plants

During early May 1987 150 target plants of each of three perennial grass species, *Agropyron repens*, *Poa pratensis* and *Phleum pratense*, were located within an 80 m × 110 m rectangular grid within the field. Target plants were at least 3 m away from all other targets but
were otherwise selected randomly. These three grasses were selected for study because they all form a dominant component of the vegetation (Table 1) and because ramets (tillers) of approximately uniform size could be easily obtained for the field experiment. All three of these grass species are commonly found in habitats ranging from chronically nutrient-impoverished as in the present study site, to those with the most fertile agricultural soils where the three grasses often co-occur as weeds or as major components of hayfields, pastures and lawns (Dore & McNeill 1980).

Target plants were carefully removed within a 10 cm diameter × 8 cm deep soil core using a bulb extractor. This procedure helped to minimize and standardize the level of disturbance around the target plants. All 450 target plants were removed over a four-day period (13-16 May) and transferred to the laboratory where they were watered as required and stored for three weeks. During this time, manipulative procedures were carried out within the field (see below). For each target plant of Agropyron and Poa, a single tiller at the three-leaf stage was selected randomly, removed and cut to a height of 10 cm. Roots were trimmed to 8 cm. For each Phleum plant, 3-5 tillers were similarly selected and cut. More tillers were selected for Phleum because preliminary work suggested that individual tillers may be subjected to higher mortality when planted back in the field.

For each of the three study species, the 150 plots in the field from which targets were removed were randomly assigned to one of 15 treatments (three levels of neighbour removal × five levels of nutrient addition) (see below) to give 10 replicates per removal × addition × species combination.

**Neighbour removal treatment**

The neighbour manipulations were carried out by spraying the vegetation around the target plant position with the broad spectrum herbicide glyphosate (N-Phosphonomethyl) glycin; tradename ‘Round-Up’) to remove (or reduce) the effects of neighbours. This herbicide does not persist in the soil (Sprankle, Meggit & Penner 1975; Torstensson 1985).

The three removal treatments were: (1) control - no vegetation sprayed; (2) 20 cm radius of vegetation sprayed around the target plant position (area = 1257 cm²); and (3) 40 cm radius of vegetation sprayed (area= 5027 cm²). A circular steel rim, 20 cm high and of appropriate radius was used during the spraying process to prevent herbicide drift onto neighbouring vegetation outside the treatment area. Before spraying, all roots, rhizomes and stolons of plants crossing the perimeter of the circular rim were severed to a depth of approximately 10 cm using a shovel to prevent the translocation of herbicide to plants outside the treated area. Throughout the experiment, any above-ground plant regrowth within the herbicide-treated areas was mechanically clipped back to ground level.

The herbicide treatment was very effective in killing all of the vegetation within the plots. Two weeks after the herbicide application, each target was replanted into its original location. Soil that was initially removed along with the target plant was also placed back into the hole that had been left by the bulb extractor. All targets had been replanted by June 8. To minimize transplant shock (and hence maximize survival), all target plants were watered periodically over the following two-week period with 200 ml of tap water.

**Nutrient addition treatment**

The nutrient addition treatment was carried out on June 11. Commercial slow-release pebble fertilizer 18-18-18 (N-P-K) (Co-op Inc., Kemptville, Ontario, Canada) was used. The five levels of application (in g/m²) were: 0 (control), 12.5, 25.0, 50.0 and 100.0. These represent a broad range of nutrient levels based on the 40 g/m² recommendation by the Ontario Ministry of Food and Agriculture for pasture land. The fertilizer was spread manually within a 20 cm radius around the target plant (1257 cm²). The same fertilizer application was repeated on July 15. All targets were monitored throughout the experiment for evidence of herbivory.

**Target harvest**

In early October (16 weeks since replanting the targets), targets (including root systems) were carefully extracted from the plots. The plants were taken to the laboratory where the soil was washed off the below-ground parts and the number of tillers was recorded. Below-ground parts consisted of just roots in Phleum but included rhizomes in Agropyron and in Poa. For each target, above- and below-ground biomass was separated, oven-dried at 100 °C for 5 days and then weighed. All biomass data thus refers to dry weight.

**Data analyses**

Two-way analysis of variance was performed on total biomass, above-ground biomass, below-ground biomass, below-ground/above-ground biomass quotient and number of tillers to determine if there were any significant effects due to the neighbour removal or nutrient addition treatments. For Phleum, initial tiller number was incorporated as a covariate. A few targets were grazed by groundhogs (Marmota monax) and were treated as missing values.
Table 2. Results from analysis of variance for plant characters of (a) *Agropyron repens*, (b) *Poa pratensis* and analysis of covariance for plant characters of (c) *Phleum pratense* affected by variation in radius of neighbouring vegetation removed and level of nutrients added. Initial tiller number (for c) was used as a covariate. Analyses were based on log-transformed data for all characters except number of tillers which was square-root-transformed. A = Above-ground biomass; B = Below-ground biomass.

<table>
<thead>
<tr>
<th></th>
<th>Total biomass</th>
<th>Number of tillers</th>
<th>A</th>
<th>B</th>
<th>B/A</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>(a) <em>Agropyron repens</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Removal radius (R)</td>
<td>8.14</td>
<td>0.001 ***</td>
<td>29.27</td>
<td>0.001 ***</td>
<td>14.50</td>
</tr>
<tr>
<td>Nutrients (N)</td>
<td>3.96</td>
<td>0.005 **</td>
<td>2.00</td>
<td>0.057</td>
<td>2.11</td>
</tr>
<tr>
<td>R × N</td>
<td>1.27</td>
<td>0.266</td>
<td>1.15</td>
<td>0.336</td>
<td>1.46</td>
</tr>
<tr>
<td>(b) <em>Poa pratensis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Removal radius (R)</td>
<td>4.70</td>
<td>0.011 *</td>
<td>50.02</td>
<td>0.001 ***</td>
<td>12.73</td>
</tr>
<tr>
<td>Nutrients (N)</td>
<td>6.28</td>
<td>0.001 ***</td>
<td>6.79</td>
<td>0.001 ***</td>
<td>3.48</td>
</tr>
<tr>
<td>R × N</td>
<td>1.23</td>
<td>0.290</td>
<td>2.31</td>
<td>0.026 *</td>
<td>1.71</td>
</tr>
<tr>
<td>(c) <em>Phleum pratense</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Removal radius (R)</td>
<td>39.30</td>
<td>0.001 ***</td>
<td>71.24</td>
<td>0.001 ***</td>
<td>50.53</td>
</tr>
<tr>
<td>Nutrients (N)</td>
<td>4.52</td>
<td>0.002 **</td>
<td>4.36</td>
<td>0.003 **</td>
<td>3.43</td>
</tr>
<tr>
<td>Initial tiller</td>
<td>6.07</td>
<td>0.016 *</td>
<td>6.47</td>
<td>0.013 *</td>
<td>7.46</td>
</tr>
<tr>
<td>R × N</td>
<td>0.95</td>
<td>0.483</td>
<td>1.94</td>
<td>0.064</td>
<td>1.72</td>
</tr>
</tbody>
</table>

* = P < 0.05; ** = P < 0.01; *** P < 0.001.

To evaluate the intensity of competitive effects under the different nutrient treatments, the percent yield reduction was calculated as \((1 - Y_0/Y_{40}) \times 100\%\), where \(Y_0\) is the total biomass (or final number of tillers) of a single target when grown in a plot having no neighbouring vegetation removed (i.e. removal control) and \(Y_{40}\) is the mean total biomass (or mean final number of tillers) of targets (of the same species) grown in plots with neighbouring vegetation removed within a 40 cm radius of the target. Linear regression analyses were used to examine the effect of nutrient level on percent yield reduction.

All analyses were performed using SAS (SAS Institute 1985) and data were log-transformed or square-root transformed (for number of tillers) to homogenize variances.

**Results**

**Target survival and flowering**

Target survival over the entire experimental period was 98% for *Phleum*, 91.3% for *Poa* and 90.0% for *Agropyron*. For each target species, mortality did not differ significantly \((P > 0.05, \text{Chi-square})\) among the three vegetation removal treatments nor among the five nutrient treatments.

No target plants of *Agropyron* or *Poa* flowered during the experiment. However, of the 147 targets of *Phleum* that survived to the end of the experiment, 37 (25.2%) flowered. The nutrient treatment had no significant effect on flowering in *Phleum* targets but the vegetation removal treatment had a highly significant \((P < 0.001, \text{Chi-square})\) effect. More than three times the number of *Phleum* target plants flowered in the highest vegetation removal plots (40 cm radius) as in the intermediate vegetation removal plots (20 cm radius) (28 versus nine plants). No *Phleum* targets flowered in the removal control plots.

Table 3. Means (and standard errors) of the below-ground / above-ground biomass quotient for target plants of *Agropyron repens*, *Poa pratensis* and *Phleum pratense* for (a) each level of neighbour removal and (b) each level of nutrient addition.

<table>
<thead>
<tr>
<th></th>
<th><em>A. repens</em></th>
<th><em>P. pratensis</em></th>
<th><em>Phl. pratense</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>a) radius of neighbour vegetation removed (cm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>4.04 (1.49)</td>
<td>1.84 (0.27)</td>
<td>3.03 (0.29)</td>
</tr>
<tr>
<td>20</td>
<td>3.51 (0.52)</td>
<td>2.55 (0.44)</td>
<td>3.65 (0.47)</td>
</tr>
<tr>
<td>12.5</td>
<td>12.5 (4.75)</td>
<td>4.62 (0.78)</td>
<td>4.75 (0.57)</td>
</tr>
<tr>
<td>b) nutrient level added (g/m²)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>4.43 (0.89)</td>
<td>2.52 (0.55)</td>
<td>3.67 (0.47)</td>
</tr>
<tr>
<td>12.5</td>
<td>7.10 (3.10)</td>
<td>2.94 (0.79)</td>
<td>3.34 (0.28)</td>
</tr>
<tr>
<td>25.0</td>
<td>5.48 (2.03)</td>
<td>3.87 (1.02)</td>
<td>3.07 (0.48)</td>
</tr>
<tr>
<td>50.0</td>
<td>15.59 (9.89)</td>
<td>3.11 (0.60)</td>
<td>4.28 (0.69)</td>
</tr>
<tr>
<td>100.0</td>
<td>4.35 (1.07)</td>
<td>4.17 (1.36)</td>
<td>6.24 (1.36)</td>
</tr>
</tbody>
</table>

*0 cm radius is control treatment;
*Means with the same letter are not significantly different \(P>0.05\) according to LSD. Where letters are not included, main ANOVA effects were insignificant \(P>0.05\).
Fig. 1. Mean (and S.E.) of a) total dry weight biomass (g) and b) final number of tillers for *Agropyron repens* targets under each of three levels of neighbour removal (40, 20 and 0 cm radius around targets) within each of five levels of nutrient addition (0, 12.5, 25, 50, 100 g/m²). Columns within each nutrient level with the same letter represent levels of neighbour removal which are not significantly different \( (P > 0.05) \) according to LSD.

Fig. 2. Mean (and S.E.) of a) total dry weight biomass (g) and b) final number of tillers for *Poa pratensis* targets under each of three levels of neighbour removal (40, 20 and 0 cm radius around targets) within each of five levels of nutrient addition (0, 12.5, 25, 50, 100 g/m²). Columns within each nutrient level with the same letter represent levels of neighbour removal which are not significantly different \( (P > 0.05) \) according to LSD.

**Effects of treatments**

The radius of neighbouring vegetation removed had a significant \( (P < 0.05) \) positive effect on total biomass and number of tillers in all three species (Table 2; Figs. 1, 2, 3). Below-ground/above-ground biomass quotient was significantly \( (P < 0.05) \) greater in the removal control plots than in the plots with neighbours removed for all three species (Table 3).

The level of added nutrients also had a significant positive effect on total biomass in all three species and on number of tillers in *Poa* and *Phleum* (Table 2; Figs. 1, 2, 3). Below-ground/above-ground biomass quotient was unaffected or inconsistently affected by the level of nutrient addition (Table 3). This contrasts with the large body of data showing a general increase in relative allocation to above-ground biomass as soil nutrient level increases (Chapin 1980). For *Agropyron* and *Poa* however, this anomaly may be a consequence of the large proportion of below ground biomass that is in rhizome.

Interactions between the two main treatment effects were all non-significant \( (P > 0.05) \) except for number of tillers in *Poa* (Table 2). Initial number of tillers in *Phleum* target plants had a significant effect \( (P > 0.05) \) on all plant characters measured except for the below-ground/above-ground biomass quotient (Table 2c).

**Yield reduction from competition**

**Agropyron repens targets**

Mean total biomass reduction resulting from competition for *Agropyron* targets across all five nutrient levels was 57%. The magnitude of biomass reduction for *Agropyron* targets decreased significantly with increas-
Mean (and S.E.) of a) total dry weight biomass (g) and b) final number of tillers for *Phleum pratense* targets under each of three levels of neighbour removal (40, 20 and 0 cm radius around targets) within each of five levels of nutrient addition (0, 12.5, 25, 50, 100 g/m²). Columns within each nutrient level with the same letter represent levels of neighbour removal which are not significantly different ($P > 0.05$) according to LSD.

Mean tiller reduction was $75\%$ overall across the five nutrient treatments and was not significantly affected by the nutrient treatment ($r^2 = 0.002; \text{df} = 49; P = 0.765$) (Fig. 4b).

**Poa pratensis targets**

Mean total biomass reduction for *Poa* targets was $43\%$ overall and showed no significant trend with increasing nutrient level ($r^2 = 0.04; \text{df} = 49; P = 0.149$) (Fig. 4c). Mean tiller reduction was $80\%$ overall across the five nutrient treatments and also showed no significant trend with increasing nutrient level ($r^2 = 0.009; \text{df} = 49; P = 0.520$) (Fig. 4d).

**Phleum pratense targets**

Mean total biomass reduction for *Phleum* targets was $74\%$ and showed no significant trend with increasing nutrient level ($r^2 = 0.003; \text{df} = 49; P = 0.730$) (Fig. 4e). Mean tiller reduction was $79\%$ overall across the five nutrient treatments and increased significantly with increasing nutrient level ($r^2 = 0.13; \text{df} = 49; P = 0.014$) (Fig. 4f).

**Discussion**

We suggest that the increase in relative allocation to below-ground biomass with increasing neighbour proximity in the present data may reflect an adaptive plastic response to selection associated with below-ground competition. In grasses, shading interactions between neighbours is minimized by relatively long, thin leaves with more of a vertical than horizontal orientation. Hence, as neighbour proximity increases among grasses, the intensity of below ground competition may increase faster than the intensity of above ground competition. Accordingly, natural selection may favour a greater plasticity in some grasses in the form of disproportionately greater allocation to below ground biomass as the local density of neighbouring grasses increases.

The greater performance of plants in cleared versus control plots reflects two components of release from competition: (1) alleviation of current competition for light and for resources that were already available in the soil; and (2) alleviation of hardships that were imposed on these plants by having been denied resources that were the objects of past competition and which had been captured and withheld by neighbours, but which have now become available from decomposition of the remains of these neighbours. It is important to note that the effects of nutrient release through this decay of neighbouring biomass may be greater under the high resource-addition treatment. Greater nutrient addition may increase the activity of decomposers, and hence, result in a higher rate of nutrient release into the soil. The percent difference in performance in cleared versus control plots may thus be accentuated by this greater decay rate. Since competition intensity here is reflected by this percent difference in performance, the above effects may bias the results in favour of greater competition intensity being indicated under the more fertile conditions.

In spite of the potential for this bias, the results do not lead to this general conclusion. The effect of nutrient level on competition intensity differed for each species and differed depending on the measure of performance used. In *Agropyron*, the extent of biomass reduction due to competition showed a declining trend with increasing nutrient level (Fig. 4a), whereas the extent of reduction in tiller production was unaffected by nutrient addition (Fig. 4b). In contrast, *Phleum* displayed a slight but sig-
significant increase in the suppressive effect of competition on tiller production (Fig. 4f) (but not biomass production, Fig. 4e) with increasing nutrient level. *Poa* showed no trend in the effect of nutrient level on the extent of either biomass (Fig. 4c) or tiller number (Fig. 4d) reduction due to competition.

The data on biomass production in *Agropyron* (Fig. 4a) are consistent with the prediction that the effect of nutrient amendments is to decrease the extent to which combined demands (of the target and its neighbours) on resources exceed the local supply (i.e. to increase the resource supply/demand ratio), and thus, to decrease the intensity of competition (e.g. Wilson 1988, p. 290). A similar effect was detected in the results of Whigham (1984). If this is regarded as a general feature of resource-rich habitats, it may lead to a general expectation that competition intensity should increase as the supply of resources decreases; e.g. "...the highest species diversities are found in nutrient-poor environments where competition must be strong" (Braakhekke 1985, p. 320). Usually however, this effect of nutrient amendments will be only temporary since, in the absence of disturbance, demands on resources can be expected eventually to increase to meet the increased supply.

C-S-R theory (Grime 1988) predicts that the general intensity of competition within vegetation increases with increase in habitat fertility, especially over a gradient ranging from intermediate fertility to highly fertile, i.e. including roughly the right half of Grime’s (1979, p. 163) ‘hump-back’ model of species density variation. According to Grime (1979), the lower species density in highly fertile habitats compared with the more intermediate fertile habitats is interpreted as a consequence of more intense competition within the highly fertile habitats. It is within this range of habitat fertility that the present study and the studies by Gurevitch (1986) and Reader & Best (1989) examine the relationship between resource level and competition intensity.

At the individual species level, the data of Gurevitch (1986) and Reader & Best (1989) support the prediction that competition is more intense at higher fertility levels. This is also marginally supported in the present study by the data on tiller production in *Phleum* (Fig. 4f). These latter data however reflect only the individual experience of *Phleum*. They do not imply that competition is categorically more intense under higher soil nutrient levels (as predicted by C-S-R theory). Competition for *Phleum* targets may be more intense at higher nutrient levels because, under these conditions, the abilities of these *Phleum* targets to deny resources to their neighbours is lower relative to the abilities of these neighbours to deny resources to *Phleum* targets. The
corollary of this is that, with decreasing soil nutrient level, *Pileum* targets experienced a decreasing competition intensity, while the neighbouring vegetation experienced an increasing competition intensity. The latter is suggested by the biomass data for *Agropyron* (Fig. 4a), for example. Under this interpretation, the general intensity of competition within the vegetation does not differ categorically across the soil nutrient gradient.

The most important result of the present study is the lack of consistent effects of nutrient level on the competition intensity experienced by the three study species. Fowler (1982) also found that variation in soil fertility resulted in a reversal in the direction of competitive dominance in a glasshouse experiment involving several coexisting grassland species. These results suggest that the intensity of competitive interaction experienced in the field may change with increasing soil fertility in a highly individualistic manner. Thus, we predict that, for some species, competition intensity should decrease when resources are added, e.g. for species that can use the abundance of resources to overtop shorter species and thus experience less intense competition from the shorter species. Conversely, these shorter species (which may include for example, those that are normally restricted to infertile conditions) would, if overtopped as above, experience more intense competition when resources are added (Aarssen 1984).

**Conclusions, limitations and future prospects**

It is reasonable to expect that certain species (or genotypes) will be excluded from certain regions of a fertility gradient because of competition. This has been confirmed from glasshouse and artificial field plot experiments (Donald 1958; Mahmoud & Grime 1976; Wilson 1988) and from some field experiments in natural vegetation (Gurevitch 1986; Reader & Best 1989). However, as illustrated by the present study, predictions concerning the general intensity of competition within multi-species vegetation cannot be adequately tested in studies based on only a single species. The results support the prediction that general competition intensity is determined primarily by the resource supply/demand ratio (as affected by the neighbour removal treatment in this study) and not by the resource supply alone (Taylor, Aarssen & Loehle 1990). Resource supply/demand ratio may be equally high in both nutrient-impoverished and nutrient-rich habitats (i.e. for a given level of disturbance). Hence, there is no reason to expect or predict any categorical difference in the general intensity or importance of competition within naturally established vegetation occurring anywhere along a habitat fertility gradient that supports viable self-perpetuating populations.

We predict that the general intensity of competition within vegetation would be greater under higher habitat fertility levels (as predicted by C-S-R theory) only if increasing habitat fertility is generally associated with: 1) lower resource supply/demand ratio, or 2) fewer opportunities for these plants to make demands on different resource units, or 3) fewer opportunities for a counter-balancing effect of beneficence between these plants. None of these general assumptions has any supporting evidence with regard to either between- or within-species competition. The first of these assumptions is counter-intuitive and probably incredible. Concerning the second assumption, Newman (1973) speculated that there may be generally fewer opportunities for niche differentiation among species as soil fertility increases. Supporting data for this however is scarce, and while niche differentiation can potentially reduce between-species competition, only rarely has it been suggested to reduce within-species competition in plants. The potential role of a counter-balancing effect between competition and beneficence (assumption 3) is largely unexplored in vegetation (Hunter & Aarssen 1988), but there is no reason to expect the significance of this to vary in any predictable way along habitat fertility gradients.

Much more experimental work with more species in both the field and the laboratory is required in order to reach a sufficient understanding of the general relationship between habitat fertility and competition intensity (both intra- and inter-specific) within natural vegetation. A number of potential limitations need to be addressed, especially for field studies (Aarssen & Epp 1990). Since competition does not occur unless plants deny resources to their neighbours, current competition in the field can only be detected if plants are currently growing and/or extracting resources from the environment. Hence, any attempt to detect current competition in, for example, a temperate grassland either during an extreme summer drought or in the ‘dead of winter’ would invariably turn up negative results since, under these circumstances, virtually the entire plant community is dormant. To conclude however, that the general competition intensity within such habitats is zero, would be completely erroneous. There is also an urgent need for studies which include an examination of neighbour effects through not only post-juvenile phases but also through the germination and seedling establishment phases of the life cycle. In some habitats, the older established components of the vegetation may show little evidence of current competition, but these plants may have been the winners in earlier intense competition involving massive mortality at the seedling and juvenile phases. Studies will also be needed which account for direct effects of neighbours on reproduction through
competition for pollinators or through negative consequences of interspecific pollen transfer (e.g. Waser & Fugate 1986; Galen & Gregory 1989; Murphy & Aarssen 1989; Randall & Hilu 1990).

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