**Marek Sammul · Kalevi Kull · Lauri Oksanen**
**Peeter Veromann**

# Competition intensity and its importance: results of field experiments with *Anthoxanthum odoratum*

**Abstract** The effect of community productivity on competition was studied in 82 permanent plots using two removal experiments with the rhizomatous perennial grass *Anthoxanthum odoratum*. The removal of neighbouring plants had a positive effect on the number of shoots and total above-ground biomass of *Anthoxanthum* but no significant effect on mean shoot biomass. The relative competition intensity coefficient (RCI) calculated from these data showed that competition intensity increased with increasing community productivity. Similarly, the importance of competition and the difference between local maximum and local average population density increased with increasing community productivity. We concluded that for *Anthoxanthum* the impact of competition is greater in high-productivity areas and that competition reduces population density. No evidence was found supporting the importance of positive interactions between plants in tundra areas.

**Key words** Importance of competition · Productivity · Removal experiments · Tundra · Wooded meadow

## Introduction

Although there have been a number of experiments analysing the relationships between competition intensity and major community parameters (Putwain and Harper 1970; Silander and Antonovics 1982; Berendse 1983;

M. Sammul (✉) · K. Kull · P. Veromann
Institute of Zoology and Botany,
Estonian Agricultural University, Riia 181,
51014 Tartu, Estonia
e-mail: marek@zbi.ee
Tel.: +372-7-428619, Fax:+372-7-383013

M. Sammul · K. Kull
University of Tartu, Institute of Botany and Ecology,
Lai 40,
51005 Tartu, Estonia

L. Oksanen
Umeå University, Department of Ecology
and Environmental Science,
901 87 Umeå, Sweden

Keddy 1989; Aerts et al. 1990; Di Tomasso and Aarssen 1991; Wilson and Tilman 1991, 1993; Gerry and Wilson 1995; Kadmon 1995; Herben et al. 1997; McLellan et al. 1997), there is as yet no general agreement on how competition changes along the principal natural gradients.

Three main hypotheses about variation of competition intensity along the productivity gradient state that either (1) competition intensity increases with increasing productivity (Grime 1973, 1979); (2) total competition intensity does not change with community productivity, but shifts from the below-ground environment in low productivity communities to the above-ground environment in high productivity environments (Newman 1973; Tilman 1982, 1988); or (3) competition intensity is minimal in plant communities of low (but not the lowest) productivity (Fretwell 1977; Oksanen 1990, 1993).

While competition intensity has received a great deal of attention, the importance of competition has remained almost unstudied. The importance of competition is defined as the relative impact of competition, among other processes, on the community composition or population dynamics (Welden and Slauson 1986; Goldberg 1994). Measurement of the importance of competition requires population-level studies in natural conditions. However, most competition research has been carried out on the level of the individual plant, or competition characteristics have been estimated from the parameters of individual plants.

Although the importance of competition is not a simple concept, the distinction between this and competition intensity has been clearly defined (see Welden and Slauson 1986). In principle, the importance of competition can be measured by four methods:

1. All major local factors that affect community composition are studied separately and compared to real community structure. From this, the relative impact of competition will be calculated. This method requires a very large number of experiments and its use is unrealistic in natural conditions.
2. Goldberg (1994) proposes a method by which the dynamics of an unmanipulated natural community is

compared to the dynamics of each single species of this community when grown separately from the others, i.e. with the dynamics of the monocultures of all species present in this community. Using monoculture densities, the "null community" is calculated and compared to the natural community (see Goldberg 1994 for details). The approach requires monocultures of each species as well as an additive mixture of all species to be established. This means that if a community consisted of e.g. 20 species, the method would involve 21 treatments, which makes it extremely labour-consuming.

3. Welden and Slauson (1986) used the relative amount of variation in experimental data caused by removal of competition as a measure of the importance of competition. This is a simple method which has unfortunately not been widely used.

4. We propose that the difference between mean real population density and maximum potential population density in a certain community be used as an estimate of importance of interspecific competition. This method is simpler than that proposed by Goldberg (1994), while its results do not apply to the whole community but only to the species studied, as does also the method suggested by Welden and Slauson (1986).

In this paper we will use the data from two very similar experiments performed in different geographical regions with the aim of studying the variation of both the intensity and importance of competition along a productivity gradient.

## Methods

### Experimental design

The data from two experiments on the perennial grass species *Anthoxanthum odoratum* (further referred to as *Anthoxanthum*), conducted in Estonia and in Norway, were included in this analysis. *Anthoxanthum* is a common plant in both study areas, and reproduces well both sexually and vegetatively. Its ramets (*sensu* Harper 1977) are mainly annual, although they sometimes survive for 2 years. The mean number of rhizome branches per ramet is 0.86 (maximum 9), mean speed of vegetative reproduction (ramets ramet$^{-1}$ year$^{-1}$) 0.5 (with a maximum of 4.5) and mean annual rhizome branch growth 4.5 mm (maximum 25 mm). There was no significant difference between the two study areas in the clonal growth pattern of *Anthoxanthum*.

The first experiment was conducted at Laelatu wooded meadow and its neighbouring meadow communities on the western coast of Estonia (58°35′15″N, 23°34′00″E). The area is a part of the Laelatu-Puhtu-Nehatu Nature Reserve. All communities studied were calcicolous grasslands. The area belongs to the boreo-nemoral zone. The mean temperature for July is 17.0°C and for January –5.0°C; the mean annual precipitation is 500 mm. A more detailed description of the site is given by Kull and Zobel (1991).

The second experiment was conducted in northern Norway, at Joatkajav'ri fjellstue, on the lower part of the Finnmarksvidda plateau (69°46′, 23°58′), at about 400–600 m above sea level (a.s.l.). This area includes tundra meadows, lichen heaths, willow thickets and birch forests, although most of the area is devoid of trees. The mean annual precipitation is 450 mm, and the mean temperature for July is 10°C and for January –10°C. A more detailed description of this area is given by Moen (1993). Some characteristics of the communities studied are given in Table 1.

In Estonia, three herb communities of different productivity and similar light conditions were chosen. Before the experiment

**Table 1** Characteristics of studied communities

| Community | Country | Mean above-ground phyto-mass (g m$^{-2}$) | Mean number of species per: | | Elevation above sea level (m) | Main dominant plant species |
|---|---|---|---|---|---|---|
| | | | 1 m$^2$ | 400 cm$^2$ | | |
| Low-productivity wooded meadow | Estonia | 700 | 32 | | 3.5 | *Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithopoda, C. flacca, Convallaria majalis* |
| Medium-productivity wooded meadow | Estonia | 900 | 37 | | 3 | *Hepatica nobilis, Brachypodium pinnatum, C. majalis, Plantago lanceolata, Primula veris, Serratula tinctoria, Briza media* |
| Abandoned hayland | Estonia | 1,100 | 28 | | 1.5 | *Dactylis glomerata, Festuca rubra, Helictotrichon pratensis, Brachypodium pinnatum, Primula veris, Carlina vulgaris, Carex tomentosa* |
| Snow-bed | Norway | 310 | | 8 | 620 | *Salix herbacea, S. polaris, Vaccinium myrtillus* |
| Willow heath | Norway | 430 | | 11 | 520 | *F. rubra, V. myrtillus, Juniperus communis, Betula nana, Empetrum nigrum* |
| Birch forest | Norway | 360 | | 13 | 480 | *V. myrtillus, Trollius europeaus, F. rubra, Trientalis europea* |
| Herb-rich meadow | Norway | 620 | | 14 | 475 | *Trollius europeaus, V. vitis-idea, Cirsium heterophyllum, Epilobium angustifolium* |
| Clearing in birch forest | Norway | 650 | | 10 | 460 | *Cornus suecica, Solidago virgaurea, Trientalis europea, Deschampsia flexuosa* |

all sites had been irregularly mown. During the experiment no mowing was done. In each community, two sites with eight permanent 30×30 cm plots (2 manipulated and 2 control plots at each site) were established.

In Norway, five communities were selected along the altitudinal gradient on a hill slope with southern exposure, within a vertical range of about 160 m (460–620 m a.s.l.). In each community, two sites with 12 permanent 20×20 cm plots (3 manipulated and 3 control plots at each site) were established, except for the lowermost community which was smaller in size and included 5 manipulated and 5 control plots.

In both experiments, the same manipulation methods were used for measurement of total competition (i.e. combination of above- and below-ground competition). In manipulated plots, the above-ground parts of all species, except for *Anthoxanthum*, were removed several (3–5) times in all seasons from 1993 to 1995. During the 1st month of the experiment, regrowth of clipped plants was quite intense. From the 2nd month their sprouting decreased remarkably and from the middle of the 2nd year of experiment it was minimal (for species other than *Anthoxanthum* approx. 2–3 shoots per plot per month). This allowed the conclusion that most below-ground parts of clipped plants had died or stopped functioning, and hence also below-ground competition was reduced. To minimise below-ground immigration of competitors from neighbouring areas, the roots were trenched to the depth of the whole humus layer (max. about 25 cm) along the edges of both manipulated and control plots with the same frequency as the clipping of above-ground parts. In most cases in Norway, trenching approached base rock, while in Estonia the depth of trenching corresponds to a depth which includes at least 95% of all roots of the herbal community (K. Kull, unpublished work). Trenching of the edges of control plots was applied in such a way as to reduce the side effects of trenching (e.g. response of *Anthoxanthum* to root damage) on experimental data.

In each plot the number of shoots was counted twice a year – at the end of June and at the end of August (except June 1994 when the number of shoots was counted only in Norway). At the end of the experiment the above-ground parts of plants were collected from all plots. The biomass obtained from control plots was separated into two fractions – "*Anthoxanthum*" and "other species". The samples were dried at 80°C for 48 h, and weighed to an accuracy of 0.01 g.

To estimate the productivity of the direct neighbourhood of target plants, the above-ground plant parts of the field layer (including litter) were collected at the time of maximum living biomass (at the end of June in Estonia and in August in Norway) in the first 2 years of the experiment (1993, 1994) from four samples of 10×30 cm per community outside the permanent plots. The samples were dried at 80°C for 48 h and weighed to an accuracy of 0.1 g. In Norway the number of species was counted in each control plot in June 1993 and in Estonia in two 1 m² plots in each community in June 1993.

Data analysis

Both data sets were standardised so that the number of shoots and biomass of *Anthoxanthum* could be presented per 1 dm².

Relative competition intensity was calculated for the number of shoots as:

$$RCI_N = (N_m - N_c)\, N_m^{-1}, \tag{1}$$

where $N_m$ is the number of shoots in manipulated plots at the end of the experiment and $N_c$ is the number of shoots in control plots at the end of the experiment.
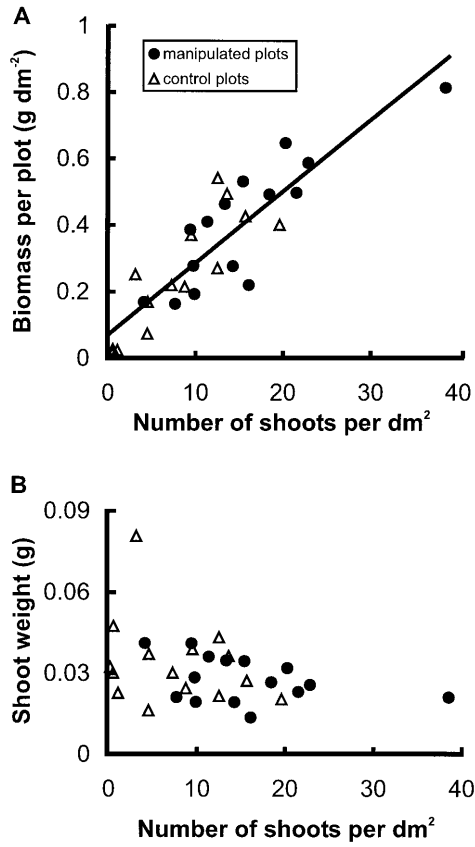
Relative competition intensity was also calculated for the total biomass of *Anthoxanthum* per plot:

$$RCI_W = (W_m - W_c)\, W_m^{-1}. \tag{2}$$

Here $W_m$ is the total biomass of *Anthoxanthum* in manipulated plots at the end of the experiment and $W_c$ is the total biomass of *Anthoxanthum* in control plots at the end of the experiment.

**Table 2** Shoot densities at the beginning and end of the experiment, and total above-ground phytomasses and shoot weights of *Anthoxanthum* at the end of the experiment, in different communities and different treatments (mean±SD) (*t* *t*-statistic for comparison of the difference between initial and final densities, *P* probability level)

| Community | Number of shoots per dm² | | | | | | | | Above-ground phytomass of *Anthoxanthum* (g dm⁻²) | | Mean shoot weight of *Anthoxanthum* (g) | |
| | Manipulations | | | | Controls | | | | Manipulations | Controls | Manipulations | Controls |
| | Beginning | End | t | P | Beginning | End | t | P | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Low-productivity wooded meadow | 0.61±0.3 | 5.9±2.9 | −3.5 | 0.039 | 0.67±0.37 | 0.3±0.1 | 3.67 | 0.03 | 0.17±0.1 | 0.01±0.01 | 0.03±0.016 | 0.025±0.016 |
| Medium-productivity wooded meadow | 1.22±0.7 | 9.64±1.4 | −15.8 | 0.001 | 0.83±0.38 | 2.5±3.3 | −1.12 | 0.35 | 0.3±0.11 | 0.05±0.06 | 0.031±0.014 | 0.03±0.03 |
| Abandoned hayland | 2.3±1.9 | 12.0±1.7 | −244 | 0.000 | 0.56±0.33 | 2.1±2.1 | −1.62 | 0.20 | 0.43±0.09 | 0.14±0.2 | 0.04±0.012 | 0.04±0.03 |
| Snow-bed | 22.5±9 | 30.7±13 | −1.69 | 0.15 | 17.8±7.18 | 17.7±8 | 0.09 | 0.93 | 0.7±0.3 | 0.4±0.2 | 0.023±0.003 | 0.024±0.005 |
| Willow heath | 12.9±5.3 | 18.8±5.2 | −4.36 | 0.007 | 11.4±7.7 | 9.9±4.7 | 0.73 | 0.49 | 0.36±0.19 | 0.25±0.12 | 0.018±0.005 | 0.028±0.013 |
| Birch forest | 10.9±8.6 | 15.3±8.9 | −4.71 | 0.005 | 12.1±3.6 | 11±3.8 | 0.69 | 0.52 | 0.46±0.29 | 0.35±0.16 | 0.03±0.01 | 0.032±0.01 |
| Herb-rich meadow | 9.6±4.4 | 16.3±7.2 | −3.02 | 0.03 | 8.0±1.9 | 11.0±6 | −1.33 | 0.24 | 0.38±0.2 | 0.46±0.38 | 0.024±0.008 | 0.038±0.012 |
| Clearing in birch forest | 10.0±5.8 | 15.4±5.5 | −3.13 | 0.035 | 7.8±2.4 | 4.6±3.2 | 2.1 | 0.1 | 0.05±0.27 | 0.17±0.18 | 0.035±0.13 | 0.027±0.024 |

**Fig. 1 A** Total biomass of *Anthoxanthum* per plot and **B** mean shoot weight of *Anthoxanthum,* in relation to the number of shoots of *Anthoxanthum* per plot in both manipulated (*filled circles*) and control plots (*open triangles*) at the end of the experiment. Plotted trendline ($y=0.02x+0.07$, $r^2=0.78$) is statistically significant at $P<0.05$. Note that there is no difference between manipulated and control plots in biomass vs. number of shoots relationship

Also, relative competition intensity was calculated for the mean shoot weight of *Anthoxanthum*:

$$RCI_{WS}=(WS_m-WS_c)\,WS_m^{-1}. \tag{3}$$

Here $WS_m$ is the mean shoot weight of *Anthoxanthum* in manipulated plots at the end of the experiment and $WS_c$ is the mean shoot weight of *Anthoxanthum* in control plots at the end of the experiment.

Importance of competition (IC) in a community for the number of shoots was calculated from the results of multivariate analysis of variance, as proposed by Welden and Slauson (1986). The relative importance of competition is the percentage of variation, accounted for by treatment effect, which equals to the sum of the squares of deviations, due to removal of neighbouring plants ($SS_{factor}$), divided by the total sum of the squares of deviations ($SS_{total}$):

$$IC=SS_{factor}\,SS_{total}^{-1}. \tag{4}$$

The difference between maximum population density and mean population density in a particular community ($R$) was calculated as:

$$R=N_{max}N_{cmean}^{-1}. \tag{5}$$

Here $N_{max}$ stands for maximum shoot density found within a given community, and $N_{cmean}$ is overall mean shoot density for the same community in control plots throughout experiment.
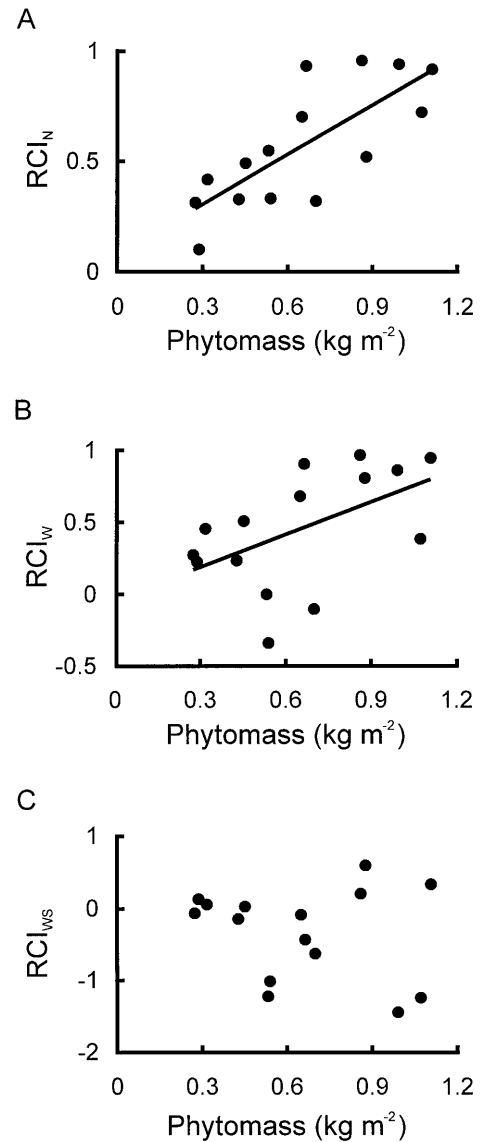


**Fig. 2** Relationships between the coefficients of relative competition intensity (*RCI*) and above-ground community phytomass for coefficients calculated from **A** number of shoots of *Anthoxanthum* per plot (*RCI_N*), **B** total biomass of *Anthoxanthum* per plot (*RCI_W*), and **C** mean shoot weight of *Anthoxanthum* (*RCI_WS*). Only statistically significant *trendlines* (at $P<0.05$) are plotted: **A** $RCI_N= 0.0008x+0.08$, $r^2=0.58$; **B** $RCI_W=0.0008x–0.04$, $r^2=0.27$

Since calculation of importance of competition involved analysis of variance, it was calculated on a per-community basis. All other coefficients were calculated on a per-site basis. To compare IC to $R$ and $RCI_N$, the last two parameters were averaged over the community.
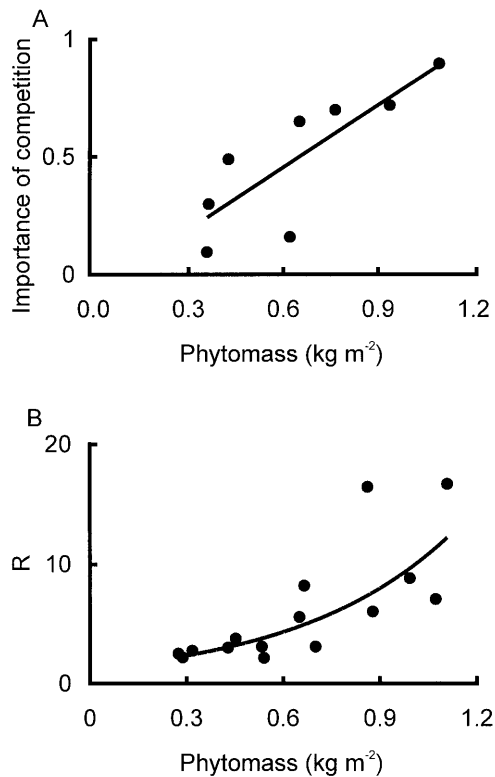
The data were analysed using the program STATISTICA (StatSoft 1995). Before analysis, all data were log-transformed. To determine treatment effects on the number of shoots and biomass of *Anthoxanthum* the nested subset ANCOVA was used, with community (8 different communities) nested in geographical region (Estonia and Norway). Site was not used as a factor in order to keep the number of replicates on a reasonable level. All factors were treated as fixed factors. Initial shoot density of *Anthoxanthum* per plot was used as a covariable.

A *t*-test for dependent samples was used to compare initial and final shoot densities. Regression analysis was applied to estimate the relation of competition parameters to community productivity.

## Results

Shoot numbers increased significantly in the manipulated plots of all communities studied except for the snow-bed (Table 2). More than 90% of new shoots in the plots were of vegetative origin. The only significant change in shoot numbers in control plots was observed at the low-productivity wooded meadow site, where the number of shoots decreased by 50% (Table 2).

Overall treatment effect was significant for the shoot numbers and total biomass of *Anthoxanthum* per plot, but not for the mean shoot weight of *Anthoxanthum* (Table 3). Per-plot analysis showed a significant correlation between the shoot density and total above-ground biomass of *Anthoxanthum* (Fig. 1A). Removal of other plan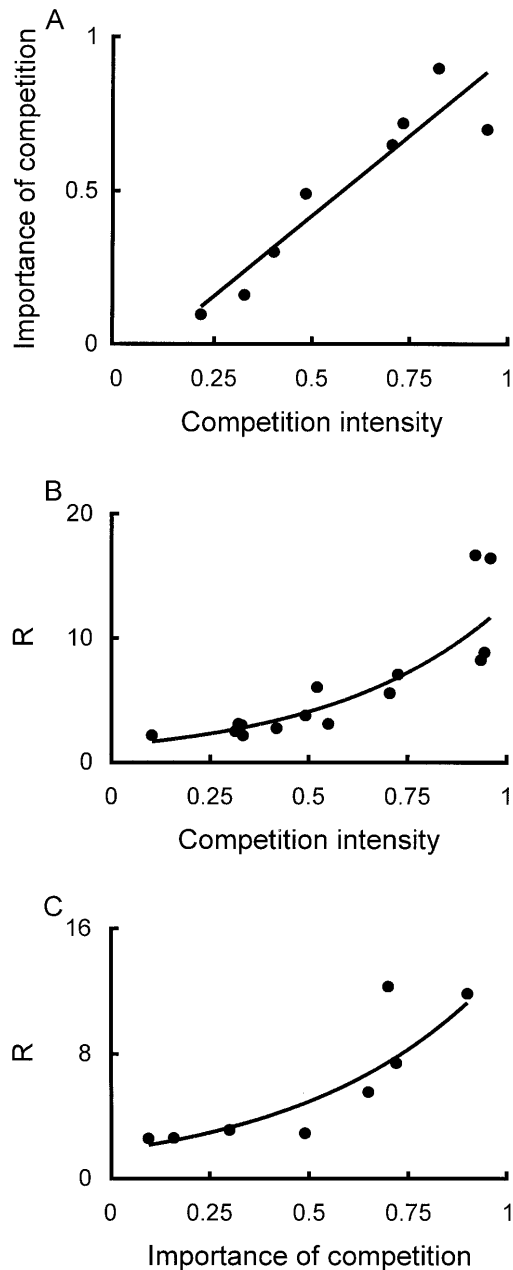ts had no effect on this relationship. No relationship was detected between shoot density and mean shoot weight either in manipulated or control plots (Fig. 1B).

There were three communities for which treatment had no effect on shoot numbers. All these communities – snow-bed, birch forest and herb-rich meadow – were in Norway. Treatment effect on the total above-ground biomass of *Anthoxanthum* per plot was significant only at the low- and medium-productivity wooded meadow sites in Estonia and in a birch forest clearing in Norway. The only site with a significant response in per-shoot biomass to removal of other plants was the herb-rich meadow in Norway.

Both $RCI_N$ and $RCI_W$ were positively correlated with above-ground community phytomass (Fig. 2). $RCI_{WS}$ had no significant relation to community phytomass. IC and $R$ were also positively correlated with above-ground community phytomass (Fig. 3). The best fit for $R$ was exponential. IC and $RCI_N$ were linearly positively correlated (Fig. 4A). The relation of $R$ to IC and $RCI_N$ was also positive but non-linear (Fig. 4B,C).

## Discussion

The few previous studies we could find in which importance of competition was measured in natural plant communities showed that competition is more important for smaller species (McLellan et al. 1997), and that intraspecific competition is more important than interspecific (Briones et al. 1996). The first result should apply more strictly to above-ground competition, where shading by bigger neighbouring plants is an influential process. The hypothesis of the greater importance of intraspecific competition compared with interspecific competition is, in theoretical works, often used as a criterion for coexistence (often called the Lotka-Volterra coexistence criterion; see e.g. MacArthur 1972; Leon and Thumpson 1975; Tilman 1982), and has also been confirmed in several experimental studies (e.g. Weiner 1980; Fowler 1982; Berendse 1983; Johansson and Keddy 1991). The third study addressing the importance of competition (Welden et al. 1988) established no relationship either between competition intensity and water stress, or between importance of competition and water stress for shrubs in northwestern Colorado. The effect of productivity on interactions between species was not studied directly in any of these papers, although water stress may be related to productivity.



**Fig. 3** The values of **A** importance of competition (IC) and **B** difference between maximum population density and average population density (*R*) in relation to community above-ground phytomass. Both *trendlines* are statistically significant at $P<0.01$: **A** IC$=0.0009x–0.074$, $r^2=0.67$; **B** $R=1.27e^{0.002x}$, $r^2=0.69$

**Table 3** Effect of removal on shoot number and total biomass of *Anthoxanthum* per plot, and mean shoot weight of *Anthoxanthum* as tested by nested sub-set ANCOVA

|  |  | Sum of squares | df | Mean square | F | P |
|---|---|---|---|---|---|---|
| Shoot number | Effect | 25.9 | 1 | 25.9 | 31.25 | <0.0001 |
|  | Error | 53.0 | 64 | 0.83 |  |  |
| Total biomass | Effect | 23.6 | 1 | 23.57 | 76.88 | <0.0001 |
|  | Error | 19.62 | 64 | 0.31 |  |  |
| Shoot weight | Effect | 0.054 | 1 | 0.054 | 0.19 | 0.66 |
|  | Error | 18.27 | 64 | 0.285 |  |  |

**Fig. 4A–C** Interrelationships between importance of competition (IC), difference between maximum population density and average population density (*R*), and relative competition intensity calculated from the number of shoots of *Anthoxanthum* (RCI$_N$). All *trendlines* are statistically significant at *P*<0.01: **A** IC=1.05*x*–0.11, *r*$^2$=0.88; **B** *R*=1.30$e^{2.28x}$, *r*$^2$=0.85; **C** *R*=1.77$e^{2.06x}$, *r*$^2$=0.81

We found in our experiment that importance of competition was higher at sites with higher productivity (i.e. at sites with larger neighbouring plants). We noted also increase in the intensity of competition with increasing productivity. This provides clear support for Grime's and Oksanen's hypotheses. It is important to keep in mind, however, that *Anthoxanthum* is a small plant and therefore expected to be more vulnerable to the presence of neighbours (Di Tomasso and Aarssen 1991; McLellan et al. 1997).

Following the hypothesis of Tilman (1988), species with low shoot/root ratios and low stature (like *Anthoxanthum*) are expected to suffer more in habitats of higher productivity even if the importance of competition remains constant, since productive habitats are characterised by more intense shoot competition. Therefore, we cannot really falsify Tilman's hypothesis. However, in our experiment we also reduced below-ground competition. Considering this, our results tend to support the idea of increase in overall importance of competition (i.e. combined above- and below-ground competition) with increasing primary productivity.

Previously, competition intensity has been shown both to increase with increasing community productivity (e.g. Wilson and Keddy 1986; Campbell and Grime 1992; Turkington et al. 1993; Bonser and Reader 1995; Gaudet and Keddy 1995; Kadmon 1995) or to have no relation to productivity (e.g. Welden et al. 1988; Di Tomasso and Aarssen 1991; Wilson and Shay 1990; Wilson and Tilman 1993; Cahill 1999). Our results show a clear relationship between community above-ground phytomass and competition intensity when the latter is calculated using population-level measures, such as number of shoots. We found no relationship between competition intensity and productivity when we used mean shoot biomass as a measure of plant performance. This confirms the recent idea that competition intensity should increase with increasing productivity when survival or community structure is assessed but not when growth of individuals is measured (Goldberg and Novoplansky 1997).

In general, intensity and importance of competition need not necessarily correlate (Welden and Slauson 1986). In our experiment this correlation was very strong (Fig. 4A). We hope to see some more publications with IC in the future to compare our results with others.

Use of *R* yields some interesting results, since it is much more sensitive than IC or RCI$_N$ on high levels of competition intensity (Fig. 4B,C). Besides, *R* has a very distinct and clear biological meaning: it indicates decrease in population density due to competition. We suppose that *R* should be clearly different for dominants and subordinants, since the population density of the former is likely to be close to maximum, while the latter can benefit significantly from free space. Comparison of the values of *R* for different species within a community can therefore be used for elaboration of competitive hierarchies.

Our results show that decrease in population density due to competition increases in case of small species (like *Anthoxanthum*) with the increasing size of neighbouring plants. However, at the low-productivity end of the gradient, tall species may lose their advantage over small species, since they do not grow so big in those communities and therefore can not outcompete smaller species. This is in agreement with empirical data from species-rich communities which are characterised by small vegetation and low productivity (Grime 1973, 1979; Kull and Zobel 1991). If species richness is a community characteristic, then in species-rich habitats no

species can have high maximum population density, and, equally low values of $R$ are expected for all species. If species richness is the result of ecological processes that reduce dominance, then high $R$ is expected for potentially dominant species in species-rich communities and low $R$ is expected for potentially subordinant species.

There has been a debate concerning the importance of positive interactions between plants, especially in arctic areas (Carlsson and Callaghan 1991; Callaway 1995, 1997, 1998). One of our experiments was carried out in a subarctic tundra area where positive interactions are assumed to be frequent (Bertness 1998). However, we found no support for the idea that *Anthoxanthum* might benefit from the presence of other species even in very harsh, windy and water-stressed snow-bed habitats. This corresponds to the results obtained for *Oxyria digyna* and *Ranunculus glacialis* (Olofsson et al. 1999).

There were enough shoots in the plots to expect occurrence of intraspecific competition. *Anthoxanthum*, indeed, has high dependence on intraspecific interactions (Berendse 1983). However, if strong intraspecific competition had occurred in our experiments, we should have discovered a strong negative correlation between the shoot density and mean shoot weight of *Anthoxanthum*. We found no such relationship (Fig. 1B), and hence, there was no evidence of the density-dependence of the population dynamics of *Anthoxanthum* in our plots.

Theoretically, the behaviour of below-ground biomass in our experiments may have been different from that of above-ground biomass. Therefore, our results could have been different, if we had measured also the below-ground biomass of *Anthoxanthum*. It is known that allocation is very flexible and removal of neighbours directly affects the ratio of red to far-red light, which is a strong determinant of the carbon allocation pattern (Fitter and Hay 1987; Ridge 1991; Larcher 1995). After removal of neighbours, the allocation pattern is expected to shift more to below-ground organs. However, *Anthoxanthum* has very short, thin rhizomes that cannot store large amounts of assimilates. Since our experiment lasted three seasons, we can also assume that there was enough time for allocation to shoots to take place.

Another issue related to the below-ground environment is that in fact we have no way to estimate how effective the reduction of below-ground competition was. Considering that there may be several ways in which above- and below-ground competition interact (Cahill 1999), the different success of their exclusion may have a strong influence on results. However, given that very few non-*Anthoxanthum* individuals emerged in our manipulated plots during the last 1.5 years of the experiment, and that all of them were removed, it is not likely that many plants survived 3 years of continuous removal of assimilating tissues. Even if their roots and rhizomes survived, their life processes (including their role in competition) must have been considerably suppressed, otherwise we would have recorded the appearance of new small shoots. The method used in this work for reducing total competition (i.e. clipping plus regular trenching) has been regarded as one of the best ways of achieving this aim (Aarssen and Epp 1990), and it proved effective during our earlier experiments.

Our results emphasise the importance of demographic competition studies, since the response of shoot number in the plot (population density) to the removal of neighbours was much stronger than that of above-ground biomass which is usually considered the best measure of plant performance. Thus we can state that at least for *Anthoxanthum*, the primary effect of competition is not a decrease in biomass but a decrease in population density due to reduction in reproductive success.

## References

Aarssen LW, Epp GA (1990) Neighbour manipulation in natural vegetation: a review. J Veg Sci 1:13–30

Aerts R, Berendse F, Caluwe A de, Schmitz M (1990) Competition in heathland along an experimental gradient of nutrient availability. Oikos 57:310–318

Berendse F (1983) Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. J Ecol 71:379–390

Bertness MD (1998) Searching for the role of positive interactions in plant communities. Trends Ecol Evol 9:191–193

Bonser SP, Reader RJ (1995) Plant competition and herbivory in relation to vegetation biomass. Ecology 76:2176–2183

Briones O, Montaña C, Ezcurra E (1996) Competition between three Chihuahuan desert species: evidence from plant size-distance relations and root distribution. J Veg Sci 7:453–460

Cahill JF (1999) Fertilization effects on interactions between above- and belowground competition in an old field. Ecology 80:466–480

Callaway R (1995) Positive interactions among plants. Bot Rev 61:306–349

Callaway R (1997) Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112:143–149

Callaway R (1998) Are positive interactions species-specific? Oikos 82:202–207

Campbell BD, Grime JP (1992) An experimental test of plant strategy theory. Ecology 73:15–29

Carlsson BA, Callaghan TV (1991) Positive plant interactions in tundra vegetation and the importance of shelter. J Ecol 79: 973–983

Di Tomasso A, Aarssen LW (1991) Effect of nutrient level on competition intensity in the field for three coexisting grass species. J Veg Sci 2:513–522

Fitter AH, Hay RKM (1987) Environmental physiology of plants. Academic Press, New York

Fowler N (1982) Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. J Ecol 70:77–92

Fretwell SD (1977) Regulation of plant communities by food chains exploiting them. Perspect Biol Med 20:169–185

Gaudet CL, Keddy PA (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. Ecology 76:280–291

Gerry AK, Wilson SD (1995) The influence of initial size on the competitive responses of six plant species. Ecology 76:272–279

Goldberg DE (1994) Influence of competition at the community level: an experimental version of the null models approach. Ecology 75:1503–1506

Goldberg DE, Novoplansky A (1997) On the relative importance of competition in unproductive environments. J Ecol 85:409–418

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242:344–347

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester

Harper J (1977) Population biology of plants. Academic Press, London

Herben T, Krahulec F, Hadincová V, Pecháčková S (1997) Fine-scale species interactions of clonal plants in a mountain grassland: a removal experiment. Oikos 78:299–310

Johansson ME, Keddy PA (1991) Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. Oikos 60:27–34

Kadmon R (1995) Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. J Ecol 83:253–262

Keddy PA (1989) Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. Can J Bot 67:708–716

Kull K, Zobel M (1991) High species richness in an Estonian wooded meadow. J Veg Sci 2:711–714

Larcher W (1995) Physiological plant ecology. Springer, Berlin Heidelberg New York

Leon J, Thompson D (1975) Competition between two species for two complementary or substitutable resources. J Theor Biol 50:185–201

MacArthur RH (1972) Geographical ecology. Harper and Row, New York

McLellan AJ, Law R, Fitter AH (1997) Response of calcareous grassland plant species to diffuse competition: results from a removal experiment. J Ecol 85:479–490

Moen J (1993) Herbivory and plant community structure in a sub-arctic altitudinal gradient. Dissertation, Department of Ecological Botany, University of Umeå

Newman EI (1973) Competition and diversity in herbaceous vegetation. Nature 244:310

Oksanen L (1990) Predation, herbivory and plant strategies along gradients of primary productivity. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, New York, pp. 445–474

Oksanen L (1993) Plant strategies and environmental stress: a dialectic approach. In: Fowden L, Mansfield T, Stoddard J (eds) Plant adaptation to environmental stress. Chapman and Hall, London, pp. 313–333

Olofsson J, Moen J, Oksanen L (1999) On the balance between positive and negative plant interactions in harsh environments. Oikos 86:539–543

Putwain PD, Harper JL (1970) Studies in the dynamics of plant populations. III. The influence of associated species on populations of *Rumex acetosa* L. and *R. acetosella* L. in grassland. J Ecol 58:251–264

Ridge I (1991) Plant physiology. Hodder and Stoughton, Kent, and The Open University, Milton Keynes

Silander JA, Antonovics J (1982) Analysis of interspecific interactions in a coastal plant community – a perturbation approach. Nature 298:557–560

StatSoft (1995) STATISTICA for Windows. StatSoft, Tulsa

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Turkington R, Klein E, Chanway CP (1993) Interactive effects of nutrients and disturbance: an experimental test of plant strategy theory. Ecology 74:863–878

Weiner J (1980) The effects of plant density, species proportion and potassium-phosphorus fertilization on interference between *Trifolium incarnatum* and *Lolium multiflorum* with limited nutrient supply. J Ecol 68:969–979

Welden CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. Q Rev Biol 61:23–44

Welden CW, Slauson WL, Ward RT (1988) Competition and abiotic stress among trees and shrubs in northwest Colorado. Ecology 69:1566–1577

Wilson SD, Keddy PA (1986) Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. Am Nat 127:862–869

Wilson SD, Shay JM (1990) Competition, fire, and nutrients in a mixed-grass prairie. Ecology 71:1959–1967

Wilson SD, Tilman D (1991) Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72:1050–1065

Wilson SD, Tilman D (1993) Plant competition and resource availability in response to disturbance and fertilization. Ecology 74:599–611