

Ann Milbau · Dirk Reheul · Benny De Cauwer  
Ivan Nijs

## Factors determining plant–neighbour interactions on different spatial scales in young species-rich grassland communities

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**Abstract** In naturally colonised species-rich grassland communities, we examined the properties of a plant's aboveground neighbourhood that affect its performance (aboveground biomass). To this end a range of neighbourhood parameters were measured: number, biomass and species richness of the neighbours, number and biomass of the conspecific neighbours, and light availability at the base of the target plant. We also determined at which neighbourhood size the strongest target plant–neighbour interactions occurred, and whether conspecific neighbours affected competitively stronger or weaker target species differently. Target plant performance varied with target identity, and was significantly affected by light availability and the number of neighbouring plants (neighbourhood density). Depending on the target species, there was also an effect of total neighbour biomass on plant performance. The target plants were most strongly affected by their neighbours within a 3-cm distance, which could account for 78% of the variance in target biomass. Number or biomass of the conspecific neighbours did not contribute to the explanation of target performance in any of the target species. Whereas in an 8-cm neighbourhood the amount of light penetration was the strongest predictor of target performance, the number of neighbours was more important in a 3-cm neighbourhood. These experimental results might be useful to extend existing neighbourhood

competition models for one or two species to multi-species competition models.

**Keywords** Competition · Conspecific neighbours · Grassland · Neighbourhood · Small-scale interactions

### Introduction

The neighbourhood approach to analysing plant competition was pioneered by Mack and Harper (1977) and involves relating the performance of an individual target plant to the number, biomass, cover, aggregation, or distance of the neighbouring species. In most neighbourhood studies (e.g. Gates 1980; Waller 1981; Weiner 1982; Watkinson et al. 1983; Goldberg 1987) a small number of neighbourhood characteristics are examined for few target species, mostly grown in monocultures or two-species mixtures under artificial conditions in greenhouses. Silander and Pacala (1985) improved this approach by trying to assess the relative importance of different neighbourhood parameters as well as the size of a plant's neighbourhood based on the number of neighbours. However, in order to achieve a detailed and complete understanding of neighbourhood competition in relation to spatial scale, multiple neighbourhood parameters measured over several distances need to be studied simultaneously in multi-species communities.

Some well-known determinants of plant competition are neighbour number (density) and biomass, which both negatively affect plant performance due to increased competition for light, nutrients and water (Julita and Grace 2002; Barot 2004; Milbau et al. 2005a). A high species-richness of neighbours might lead to complementary resource use (Wardle 2001), which could increase the amount of resources consumed by the neighbours, and thus decrease the amount left available to the target plant (Foster et al. 2002; Fridley 2003). Target performance would therefore also decrease as the species-richness of the neighbouring community increases.

A. Milbau (✉)  
Botany Department, Trinity College Dublin,  
Dublin 2, Ireland  
E-mail: milbaua@tcd.ie  
Tel.: +353-1-6083746  
Fax: +353-1-6081147

D. Reheul · B. De Cauwer  
Department of Plant Production,  
Faculty of Bioscience Engineering, Ghent University,  
Coupure Links 653, 9000 Gent, Belgium

I. Nijs  
Research Group of Plant and Vegetation Ecology,  
Department of Biology, University of Antwerp,  
Universiteitsplein 1, 2610 Wilrijk, Belgium

Little is known about the size of a plant's neighbourhood in which most of these plant–neighbour interactions occur. Although competition is primarily local, more distant belowground neighbours are most likely to be important (Molofsky 1999; Casper et al. 2003). Additionally, recent research on plant competition has indicated that intraspecific competition affects weaker and stronger competitors differently. Stoll and Prati (2001) and Monzeglio and Stoll (2005) found that weaker competitors (those species with the lowest biomass) increase their fitness when grown in the neighbourhood of conspecifics, while stronger competitors are suppressed. This implies that the spatial arrangement of plants in a community can be an important determinant of species performance and coexistence.

A previous experiment (Milbau et al. 2005b) gave us the opportunity to examine plant–neighbour interactions with different neighbourhood sizes in recently colonised species-rich grassland communities after a severe disturbance. In the current study we address the following questions:

1. What properties of a plant's neighbourhood affect its performance?
2. How big is a plant's neighbourhood?
3. Does intraspecific competition affects stronger and weaker competitors differently?

## Materials and methods

### Colonisation of the containers

One hundred and forty-four containers (20 × 15 × 14.5 cm deep) containing the remains of plant communities that were previously exposed to severe heat and drought (Milbau et al. 2005b), were placed in species-rich grassland to be colonised over almost a 1-year period (summer 2003 to summer 2004). In the previous experiment these containers had been planted with monocultures of eight different grass species (18 containers per species; 30 plants per container) and were subsequently exposed to a simulated heat wave (infrared irradiation) in the field. At the end of the experiment most plants had died, with 77% of the containers containing less than five surviving plants.

On 8 September 2003 the containers were randomly placed in a closed array in species-rich grassland. After winter, survivorship of the original monocultures had further decreased and new plants were allowed to establish from seed. On 19 July 2004, at the peak of the growing season, a vegetation survey was carried out on all containers to determine the number of colonising species and individuals. One thousand eight hundred and nine new plants had established, belonging to 19 species. The most abundant colonisers were: *Trifolium repens* L., *Holcus lanatus* L., *Juncus bufonius* L., *Agrostis tenuis* Sibth., *Poa annua* L., *Achillea millefolium* L., *Poa trivialis* L. and *Sonchus asper* (L.) Hill. Except for *J.*

*bufonius*, all species were common in the surrounding vegetation. Because grasses were the most abundant, the four most frequent grass species (*A. tenuis*, *H. lanatus*, *P. annua*, and *P. trivialis*) were chosen as target species for the neighbourhood experiment. For each target species, containers of different previous monocultures were chosen in which a target plant was located near the centre. Only containers with less than five surviving monoculture plants were selected, on condition that those survivors were positioned outside the study area of 8 cm around the target plant. For *A. tenuis*, *H. lanatus*, *P. annua* and *P. trivialis* 22, 23, 14 and 13 containers respectively were selected for the neighbourhood experiment.

### Neighbourhood experiment

On 4 and 5 August 2004, in each container the target individual was cut, its position (centre of the plant) marked on transparency paper, and its standing above-ground biomass (hereafter “target performance”) determined after oven-drying for 48 h at 75°C. After removing the target, the extent to which it was shaded by its neighbours was estimated by measuring photosynthetic photon flux density (PPFD) above the canopy and at the centre of the target at 2 cm above the soil surface, yielding percentage light penetration (hereafter “light availability”). To this end, a small quantum sensor with a gallium arsenide photodiode (Pontailier 1990) was used, attached to a thin metal rod. Subsequently all neighbouring plants within 8 cm of the target plant were identified, their standing biomass measured, and their position within the circle measuring 16 cm in diameter noted. Marks on transparency paper allowed us to measure the axes connecting the centre of the target plant to those of its neighbours.

### Analyses

Prior to the planned analyses, we checked the data for possible remainder effects from the drought experiment. An ANOVA with target performance as dependent variable, target identity and original monoculture identity as fixed factors, and survival of the drought experiment as covariable showed no history effect (monoculture identity or survival) of the containers on target performance ( $P > 0.05$  in all cases). There was only an (expected) significant effect of target identity on target biomass ( $F_{3,42} = 22.189$ ,  $P < 0.001$ ).

From the raw data we calculated the number, the species richness, and the total biomass of neighbouring plants within neighbourhoods of different radii (2, 3, 4, 5, 6, 7 and 8 cm from the target plant). Also, the number and total biomass of conspecific neighbours within the specified radii were determined. This allowed us to explore which radius gave the best fit for predicting target performance from the observed neighbourhood parameters.

As a first step, we determined which neighbourhood parameters significantly affected target plant performance in an 8-cm neighbourhood. To this end we performed a multiple regression with a stepwise removal procedure ( $F_{in} = 4$ ,  $F_{out} = 3.9$ ; Glantz and Slinker 2001). The independent variables used were the measured neighbourhood parameters from the 8-cm radius (number, biomass and species richness of all neighbours; number and biomass of conspecific neighbours; light availability), three dummy variables to encode target identity (“effects coding” method:  $T_{At} = 1$  if species *A. tenuis*,  $T_{At} = -1$  if species *P. trivialis*,  $T_{At} = 0$  otherwise;  $T_{Hl} = 1$  if species *H. lanatus*,  $T_{Hl} = -1$  if species *P. trivialis*,  $T_{Hl} = 0$  otherwise;  $T_{Pa} = 1$  if species *P. annua*,  $T_{Pa} = -1$  if species *P. trivialis*,  $T_{Pa} = 0$  otherwise; Glantz and Slinker 2001), and all species by neighbourhood parameter interactions. Effects coding provides a means by which n-way analysis of variance problems can be addressed using multiple regression. We used it because it produces results that are immediately comparable with standard ANOVA procedures when interactions are included. With effects coding, the intercept is equal to the grand mean of the dependent variable and each regression coefficient represents deviations from the grand mean, thereby reflecting a treatment effect (Pedhazur 1997). Only data from the 8-cm radius were used, because we would not be able to interpret the results if the neighbour parameters of all radii and their interactions were included in one analysis.

As a second step, we tried to determine the neighbourhood size in which the strongest target–neighbour interactions occurred. To this end a multiple regression with stepwise removal was performed with only the variables that were retained in the first model, but now the values from each radius were used. Again all species–parameter interaction terms were added.

Target biomass was  $\log_{10}$ -transformed and percentage of light penetration was arcsine transformed to improve linearity of the relationships and normality of the residuals. Statistical analyses were performed with SPSS 13.0 (SPSS, Chicago, IL, USA).

## Results

What properties of a plant’s neighbourhood affect its performance?

The four species differed in their overall performance. *A. tenuis* reached the highest aboveground biomass of  $1.72 \text{ g plant}^{-1}$ , followed by *H. lanatus* with  $0.70 \text{ g plant}^{-1}$  and *P. annua* with  $0.34 \text{ g plant}^{-1}$ . *P. trivialis*, with an average of  $0.11 \text{ g plant}^{-1}$ , showed the lowest performance. In the 8-cm neighbourhoods, target performance was significantly affected by target identity (in *A. tenuis* biomass was higher, and in *P. trivialis* lower than overall average target biomass), light availability (positive influence), and the number of neighbours (negative influence; Table 1). There were also significant interactions between target identity and the number of neighbours and between target identity and neighbour biomass, indicating that both the effects of neighbour number and neighbour biomass depended on target species (see Fig. 1a for neighbour biomass). This regression model explained 66% of the variance in target performance and was highly significant ( $F_{5,64} = 25.044$ ,  $P < 0.001$ ). According to the tolerance values there were no problems with multicollinearity (tolerance statistics all far above 0.2; Menard 1995). Neighbour biomass (main effect), species richness, and the number and biomass of conspecific neighbours did not significantly contribute to the regression model.

How big is the plant’s neighbourhood?

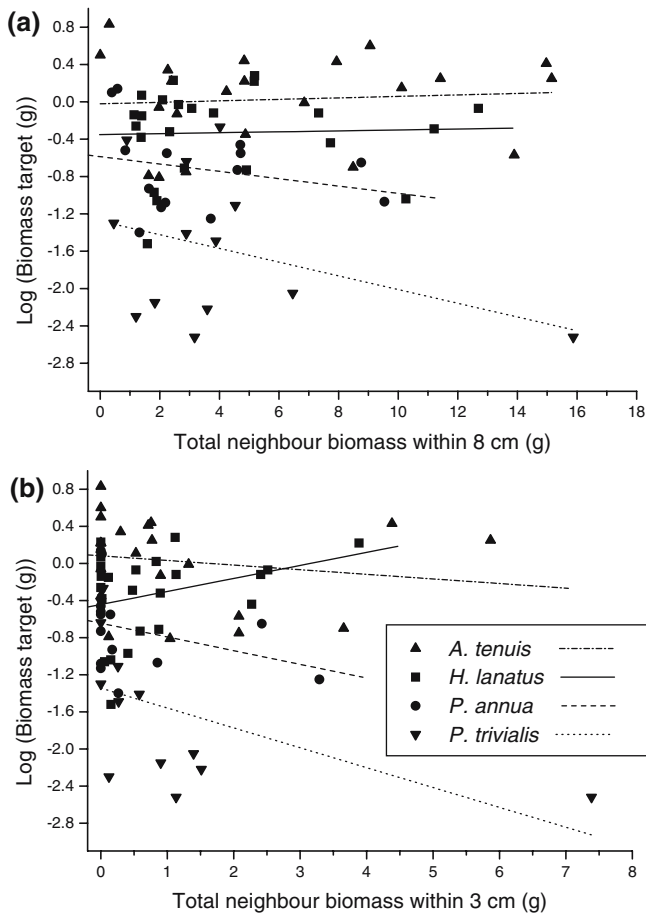
A second stepwise multiple regression was performed with the values from each radius (2, 3, 4, 5, 6, 7 and 8 cm) for the neighbourhood parameters retained from the first model, to determine the neighbourhood size in which the neighbourhood parameters most strongly affected target performance. The variables kept in the best model were the dummy variable  $T_{At}$ , light availability, the number of neighbours within 3 cm, and two species

**Table 1** Results of stepwise multiple regression with target biomass as dependent variable and as independent variables: target species (encoded by three dummy variables:  $T_{At}$ ,  $T_{Hl}$  and  $T_{Pa}$ ); number, biomass, and species richness of the neighbours within 8 cm of the target; number and biomass of the conspecific neighbours within 8 cm; light availability and all interactions with target species

Source of variation	Unstandardised coefficients	Standardised coefficients	<i>t</i>	<i>P</i>	Tolerance
(Constant)	-1.181	–	-4.251	< 0.001	–
$T_{At}$	0.301	0.267	2.198	0.032	0.357
Light availability	0.462	0.302	3.982	< 0.001	0.919
Number of neighbours (8 cm)	-0.046	-0.230	-2.921	0.005	0.856
$T_{Hl} \times$ number (8 cm)	0.027	0.247	3.057	0.003	0.809
$T_{At} \times$ biomass (8 cm)	0.040	0.236	2.080	0.042	0.411

The variables retained in the model are shown with their coefficients, significance and tolerance

Dummy variables:  $T_{At} = 1$  if species *A. tenuis*,  $T_{At} = -1$  if species *P. trivialis*,  $T_{At} = 0$  otherwise;  $T_{Hl} = 1$  if species *H. lanatus*,  $T_{Hl} = -1$  if species *P. trivialis*,  $T_{Hl} = 0$  otherwise;  $T_{Pa} = 1$  if species *P. annua*,  $T_{Pa} = -1$  if species *P. trivialis*,  $T_{Pa} = 0$  otherwise



**Fig. 1** Relationships between target performance and the biomass of all neighbours within **a** 8 cm and **b** 3 cm of the target plant, for the four target species

by neighbour biomass (3 cm) interaction terms (Table 2). This model explained 78% of the variation in target performance ( $F_{5,64} = 44.332$ ,  $P < 0.001$ ). Similar to the first model, performance increased with light availability, and *A. tenuis* and *P. trivialis* had respectively a higher and a lower biomass than the overall average. The number of neighbours affected target performance the most in a 3-cm radius neighbourhood, which was also found for neighbour biomass, but the

nature of the latter effect depended on target species. According to Table 2, performance of *H. lanatus* increased with neighbour biomass ( $0.259 \times (+1) + (-0.158) \times 0$ ), whereas the influence was negative in *P. annua* ( $0.259 \times 0 + (-0.158) \times (+1)$ ) and *P. trivialis* ( $0.259 \times (-1) + (-0.158) \times (-1)$ ), and not significant in *A. tenuis* ( $0.259 \times 0 + (-0.158) \times 0$ ) (see also Fig. 1b). The positive effect of neighbour biomass on *H. lanatus* might be due to facilitation, which is extremely common in plant communities (Cheng et al. 2006).

Comparison of the standardised regression coefficients for the 8- and 3-cm neighbourhoods (Tables 1, 2) suggests that the relative importance of the different parameters in determining target performance changes with neighbourhood size. In the 8-cm neighbourhood light availability had the largest standardised regression coefficient, indicating that changes in this parameter have the largest effect on target performance. On the other hand, in the 3-cm neighbourhood the number of neighbours was the most important determinant of performance, followed by target species ( $T_{At}$ ).

Does intraspecific competition affect stronger and weaker competitors differently?

Neither number nor biomass of conspecific neighbours was retained in our first regression model. This implies that number and biomass of all neighbouring plants together were more important in determining target performance than number and biomass of only the conspecific neighbours. In addition, no significant interactions between number or biomass of conspecific neighbours and target species were observed, indicating that the influence of conspecific neighbours did not differ among the target species.

## Discussion

What properties of a plant's neighbourhood affect its performance?

The results from our pot experiment showed that most (almost 80%) of the variation in individual plant per-

**Table 2** Results of stepwise multiple regression with target biomass as dependent variable and as independent variables:  $T_{At}$ , light availability, number of neighbours (for the different radii: 2–8 cm),

target species ( $T_{At}$ ,  $T_{Hl}$  and  $T_{Pa}$ )  $\times$  number of neighbours (2–8 cm), and target species ( $T_{At}$ ,  $T_{Hl}$  and  $T_{Pa}$ )  $\times$  neighbour biomass (2–8 cm)

Source of variation	Unstandardised coefficients	Standardised coefficients	T	P	Tolerance
(Constant)	-1.120	-	-5.579	< 0.001	-
$T_{At}$	0.464	0.412	6.232	< 0.001	0.802
Light availability	0.403	0.264	4.232	< 0.001	0.902
Number of neighbours (3 cm)	-0.163	-0.414	-6.305	< 0.001	0.811
$T_{Hl} \times$ biomass (3 cm)	0.259	0.403	4.810	< 0.001	0.500
$T_{Pa} \times$ biomass (3 cm)	-0.158	-0.219	-2.538	0.014	0.472

The variables retained in the model are shown with their coefficients, significance and tolerance.  $T_{At}$ ,  $T_{Hl}$  and  $T_{Pa}$  are dummy variables to encode target species

Dummy variables:  $T_{At} = 1$  if species *A. tenuis*,  $T_{At} = -1$  if species *P. trivialis*,  $T_{At} = 0$  otherwise;  $T_{Hl} = 1$  if species *H. lanatus*,  $T_{Hl} = -1$  if species *P. trivialis*,  $T_{Hl} = 0$  otherwise;  $T_{Pa} = 1$  if species *P. annua*,  $T_{Pa} = -1$  if species *P. trivialis*,  $T_{Pa} = 0$  otherwise

formance in young, species-rich grassland communities could be explained by target identity, light availability, neighbour number and neighbour biomass (the latter depending on the species). These characteristics were more important than the parameters that represent the identity of the neighbours (neighbour species richness and number and biomass of the conspecific neighbours). The retained parameters are all rather easy to measure and might be used to extend neighbourhood competition models for one species (e.g. Molofsky 1999; Purves and Law 2002) to multi-species models.

The number of neighbours within a certain distance from the target (or neighbour density) negatively influenced target performance, and this characteristic became relatively more important in a smaller neighbourhood (see standardised regression coefficients). Because neighbour number was not correlated with light availability (data not shown) and because there was no water shortage during the experiment, we might suppose that the negative effect of neighbour number on target performance worked at least partly through increased competition for soil nutrients. This result supports the idea that in this system competition for soil resources might be stronger than competition for light (Casper and Jackson 1997), especially on a small neighbourhood scale.

A possible explanation why species richness was not retained in the regression model is that the effects of this parameter on target plants are indirect (Milbau and Nijs 2004), which makes it a less important predictor. For example, high neighbour richness might reduce target performance by means of reduced light availability, because diverse communities absorb more light through better three-dimensional space filling and greater biomass (Spehn et al. 2000; significant negative correlations between species richness and light in the 4-, 5- and 6-cm neighbourhoods, data not shown). High species richness might also indirectly reduce target performance by affecting nutrient availability through complementarity for resource use (Dukes 2001).

Most of the variation in target performance was accounted for by the measured neighbourhood characteristics. However, other factors such as variation in emerging time and initial size (Wyszomirski et al. 1999; Weigelt et al. 2002), genetic differences among individuals and environmental heterogeneity (Fowler 1984) could be incorporated into the model to achieve a more accurate description of the effects of neighbourhoods on plant performance.

#### How large is the plant's neighbourhood?

In our experiment, target performance was best predicted by neighbourhood characteristics measured within 3 cm of the target plant. Comparable results were obtained by Mack and Harper (1977) and by Silander and Pacala (1985), who found that radii of 2 and 5 cm respectively gave the best fit for their competition

models. The neighbourhood sizes in spontaneously colonised communities thus seem to be comparable with the neighbourhood sizes observed in studies with artificially constructed communities or monocultures. Because plants interact primarily with close neighbours, we would even expect a better prediction in a 2-cm neighbourhood. A possible explanation for the relatively small size of the best neighbourhood radius for predicting plant performance is that neighbours located more than 3 cm from the target plant may on average have a net positive effect on that plant by depressing the growth of the closer neighbours (Silander and Pacala 1985). Neighbour number and biomass became relatively less important in a larger neighbourhood, in which a larger part of the variation in target performance was explained by light availability. This suggests that target plant–neighbour interactions become less intense as the distance between them increases. Similar results are found in studies on belowground zones of influence (e.g. Casper et al. 2003), in which the probability of resource uptake or competitive interaction with a particular neighbour declines with distance from the stem, although considerable uptake at great distances from the stem is still possible.

#### Does intraspecific competition affect stronger and weaker competitors differently?

Whereas the total number and total biomass of the neighbouring plants significantly affected target performance, no significant effects were found if only the conspecific neighbours were considered. Also, the interaction terms (target species  $\times$  number of conspecifics; target species  $\times$  biomass of conspecifics) were not retained, so our data do not confirm the hypothesis, based on Stoll and Prati (2001) and Monzeglio and Stoll (2005), that conspecific neighbours have a negative effect on stronger competitors and a positive effect on weaker competitors. However, because our experiment was not specifically designed to study the role of conspecifics, we could not separate the effect of more or less conspecific neighbours from the effect of more or less neighbours in total. So, a possible effect of the conspecific neighbours might have been blurred by the covariation of total neighbour number with number of conspecifics (data not shown) and remained undetected. Nevertheless, in our analyses neighbour density (and neighbour biomass) seem to prevail over the conspecific parameters in determining target plant performance, suggesting that the effect of conspecifics was indeed relatively unimportant in recently colonised grassland communities.

In conclusion, we demonstrated that individual plant performance in young, species-rich grassland communities could be well explained by easily measurable parameters (target identity, light availability, number and biomass of all neighbours within a 3-cm distance). The influence of the conspecifics seemed to be of minor

importance compared with the overall neighbour density and biomass. The neighbourhood in which the strongest target–neighbour interactions occurred was small (3-cm radius), with neighbour density being the strongest predictor of target performance.

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