The relationship of total and per-gram rankings in competitive effect to the natural abundance of herbaceous perennials

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Summary

1 Using a field experiment and a garden experiment, I estimated the rankings in total and per-gram competitive effect of non-woody perennial old-field species.

2 Total competitive effects were defined as the relative reduction in growth of a target from no-neighbour to with-neighbour conditions. Per-gram competitive effects were defined as the per-unit relative reduction in target growth among increasing neighbour densities, and were determined from the shape of a nonlinear curve fit through a distribution of normalized target performance against neighbour mass.

3 In both experiments, mean total competitive effect differed significantly among species, indicating a strong competitive hierarchy. In the garden experiment only species at opposite ends of the ranking differed significantly in per-gram competitive effect, resulting in a weaker competitive hierarchy based on this measure.

4 Nonetheless, rankings of per-gram competitive effect were more strongly correlated with rank in abundance than were rankings of total competitive effect.

5 Per-gram competitive effect may be more predictive of natural abundance than total competitive effect for at least two reasons. The effects of neighbour abundance on targets are nonlinear, and unlike total effects, per-gram estimates of competitive effect may therefore indicate how competition changes over time with changing neighbour densities. Also, if higher per-gram competitive effect reflects higher per-unit nutrient uptake rates, it would probably be advantageous to a species throughout the individual's life span, rather than only when the individual is larger than its surrounding neighbours.

Key-words: additive experiments, boundary analysis, competitive hierarchies, competitive suppression, field experiment

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Introduction

It is widely predicted that if species differ in competitive ability within a community, such differences will have a significant influence on the relative abundance of those species (e.g. Hutchinson 1957; Grime 1977; Tilman 1977, 1980; Huston & Smith 1987). Considering individual-level competitive ability, plants may differ in their ability to suppress neighbours (often called competitive effect) or in their ability to tolerate suppression from neighbours (competitive response; Goldberg & Werner 1983). Competitive effect and response are not necessarily correlated (Goldberg & Landa 1991; Keddy *et al*. 1994) and the influence of each component on natural abundance has yet to be determined. Nonetheless,

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total competitive effect (here defined as the relative reduction in performance of a target species when grown at high compared to low densities of neighbouring species) is often positively correlated with size (Gaudet & Keddy 1988, 1995) and plant size may be a useful general predictor of the magnitude of competitive effect. Indeed, ultimate plant size is often considered an important trait when modelling the potential of a species to become dominant (Huston & Smith 1987; Kohyama 1992). However, if plants change relative size throughout their lives, beginning smaller and becoming larger than their competitors, then large total competitive effects would be beneficial only when individuals are adults, not seedlings. In environments where individuals must germinate and grow under an intact canopy, competition commonly occurs from seedling through to adult stages of life (Wilson 1994; but see Callaway 1995). If a small individual in competition for resources with larger neighbours has greater rates of per-unit resource

uptake (i.e. is a better per-gram competitor), it may, in fact, have an advantage over the long term because it would acquire more resources relative to its size. These size-independent, per-unit effects, if they do confer an advantage, would be relevant throughout the life of the individual, rather than only at the adult stage.

Plant species have been shown to differ in their per-unit root absorption capacity (reviewed by Chapin 1980 and Casper & Jackson 1997). Differences in *per-gram* competitive effect (the per-unit relative reduction in target growth as neighbour densities increase) are commonly found among plants in well-controlled glasshouse environments (e.g. Goldberg & Fleetwood 1987; Gordon *et al.* 1989; Goldberg & Landa 1991; Keddy *et al.* 1994; Gaudet & Keddy 1995). However, the biological significance of these per-gram differences has often been questioned because of the overriding influence of plant size (Goldberg 1996).

This paper tests for such significance by comparing rankings based on total and per-gram competitive ability with patterns of natural abundance. If competition influences the final abundance of species, then abundance should be linked to rankings in competitive ability. While competitive ability may be defined in many ways (Connolly 1986; Grace 1995), perhaps the most utilitarian definition would be the one that best predicts the 'outcome of competition' (*sensu* Welden & Slauson 1986; Gibson *et al.* 1999). I used an additive experimental design, which avoids problems associated with replacement series designs (see Connolly 1997; Jolliffe 2000), and also allows a comparison between total and per-gram competitive effects.

If differences in per-gram competitive effect are biologically significant, then such differences should be detectable under field conditions (i.e. with natural background noise). Miller & Werner (1987) found that although differences between species were small, there was a strong relationship between rank in per-gram competitive effect and abundance. It remains to be seen whether estimates of total competitive effect are stronger or easier to attain, and whether they provide the same or possibly more accurate results.

I examined the rankings for an old-field community in both a field and a garden experiment. Here, I focus on competitive effect; competitive response, the other component of competitive ability, is described elsewhere (Howard & Goldberg in press). I address two

questions: (i) how do the magnitude and rank order of competitive effect differ among old-field perennials on a total and a per-unit basis? and (ii) how closely do rankings of total and per-gram competitive effect compare to rankings of natural abundance?

Methods

FIELD EXPERIMENT

The field experiment was conducted in a long-established (> 70 years) old-field in the E. S. George Reserve in Pinckney, Michigan, USA (42°27′27″ N, 84°1′11″ W). During the spring of 1995, I chose 150 40 cm diameter plots; 30 dominated by each of five neighbour species: *Centaurea maculosa* Lam., *Chrysanthemum leucanthemum* L., *Danthonia spicata* (L.) F. Beauv., *Hieracium piloselloides* Villars., and *Poa compressa* L. (hereafter generic name only; see Table 1 for growth forms). I chose plots with an initially high density of the selected neighbour species so that subsequent weeding would provide lower density treatments.

All species other than the selected neighbour were removed from plots twice during 1995. By the time treatments were applied, all plots had therefore developed high-density monocultures of the neighbour species. I transplanted adult *Hieracium* and *Centaurea* collected from other locations in the same field into each plot between 8 and 10 October 1995 (*n* = 15 plots for each target-neighbour species combination). Targets were chosen for their relatively high abundance and ease of transplanting. Each transplant was collected in an intact soil core (5 cm diameter × 15 cm deep) and this was planted in a hole of the same dimensions in the centre of a plot. All targets were measured at planting and initial biomass was estimated by collecting, measuring, drying and weighing an additional 20 individuals of each species (Table 2).

Density treatments were applied on 18–23 May 1996 when neighbours were clipped to a preset and randomly designated density (5 plots of zero density, 10 plots of increasing neighbour densities for each target-neighbour combination). The few weeds that returned to the plots were removed from 3 to 11 July. All targets and neighbours were harvested between 16 and 20 October 1996. Plants were dried at 60 °C to constant weight and weighed to the nearest 0.001 g.

Table 1 Neighbour species used in the field (F) and garden (G) experiments. Average above-ground biomass (AB, *n* = 2) for the high density plots in the field experiment and the average high values for *N* (*n* in parentheses), an index of density (see text), in the garden experiment were determined for each neighbour species

Neighbours	Experiment	Growth form	AB (F) (g m⁻²)	*N* (*n*) (G)
Achillea millefolium	G	Forb, rosette	–	14.6 (10)
Centaurea maculosa	F, G	Forb, rosette	106.4	28.3 (11)
Chrysanthemum leucanthemum	F, G	Forb, decumbant	106.0	15.0 (7)
Danthonia spicata	F	Grass, bunch	394.5	–
Hieracium piloselloides	F, G	Forb, rosette	90.4	7.0 (7)
Hypericum perforatum	G	Forb, erect	–	1.8 (12)
Poa compressa	F, G	Grass, interstitial	216.4	1.2 (11)

Table 2 Stepwise linear regression equations for biomass of target species in the field experiment. These were used to estimate mean initial above-ground biomass (± SEM, $n = 75$ for *Centaurea*, $n = 74$ for *Hieracium*). Mean final above-ground biomass was measured for all zero-neighbour plots ($n = 21$ for *Centaurea*, $n = 24$ for *Hieracium*). Regressions: m, target mass; lf, total summed leaf lengths (cm) of all leaves on the individual; d, the diameter (mm) of the stem and leaf bases at their point of attachment (both targets are rosette species)

Species	Equations for initial biomass	R^2	Estimated initial mass (g)	Final mass (g)
Centaurea maculosa	$m = -0.167 + 0.0028 \times lf + 0.07 \times d$	0.87	0.138 (± 0.009)	0.544 (± 0.111)
Hieracium piloselloides	$m = -0.089 + 0.005 \times lf + 0.0295 \times d$	0.88	0.167 (± 0.008)	0.799 (± 0.089)

Analysis

First, I quantified total competitive effect using an index based on the relative reduction in growth from no-neighbour to with-neighbour conditions. The 'relative interaction intensity' (RII) is a variation of the commonly used 'relative competition intensity' (RCI; see Grace 1995), however, RII is symmetrical around zero and constrained by +1 (facilitation) and –1 (competition), while RCI is asymmetrical around zero because facilitative interactions are not standardized (Markham & Chanway 1996). Although all mean effects in these experiments are competitive, some individuals were positively affected by neighbours and thus the use of RII provides a balanced estimate of all interactions. Relative interaction intensity is calculated as (Suding & Goldberg 1999):

$$RII = \frac{T_{+N} - T_{-N}}{\max |T_{-N}| \text{ or } |T_{+N}|} \qquad \text{eqn 1}$$

where T_{-N} is the performance of the target in the absence of neighbours, here the mean of the five replicates. T_{+N} is the performance of the target in the presence of neighbours. Target performance is the absolute change in mass from planting to harvest. I used the five highest densities for each neighbour and thus calculated five values of RII for each target-neighbour combination. This index estimates the total effect of neighbour presence, without standardizing for neighbour size. A mean RII significantly less than zero indicates a competitive interaction.

Next, I estimated the per-gram competitive effect of neighbours by fitting a nonlinear curve through a plot of target performance against neighbour standing crop. With added neighbour mass, target performance generally decreases in the standard reciprocal-yield relationship (Watkinson 1980; Weiner 1982):

$$\frac{T}{T_0} = \frac{1}{1 + cN} \qquad \text{eqn 2}$$

where T is the target growth, T_0 is the target growth with no neighbours (the Y-intercept), N is neighbour biomass, and c is a decay constant that describes the shape of the curve (equivalent to the slope in a linear model). Note that target performance is scaled to the proportion of growth under no-neighbour conditions. The magnitude of per-gram competitive effect is reflected in the shape of the curve; larger values of c indicate a higher competitive effect of neighbours.

The second method of estimating per-gram competitive effect identifies the upper boundary of the point distribution of target performance vs. neighbour abundance rather than the centre of the point distribution, as in the method above. Also called an envelope effect (Firbank & Watkinson 1987; Goldberg 1987; Fowler 1990) and a factor-ceiling distribution (Thomson *et al.* 1996), the presence of a boundary in this case implies that factors other than competition may be limiting. Thus, at low neighbour abundance, targets will not necessarily grow to the maximum size predicted by competitive release. At higher neighbour abundance, competitive effects become the main limiting factor and dictate a smaller target size. The resulting point distribution would fall below the curve that describes the effect of competition from neighbours, hence the boundary phenomenon. I used the partitioned regression techniques of Thomson *et al.* (1996) to estimate the upper boundary of the curve of target performance against neighbour abundance. The partitioned regression entails fitting a new line to only the positive residuals from the first nonlinear regression, thus bringing the line closer to the upper boundary of points. Note that statistical methods that can estimate and differentiate among boundary distributions have yet to be developed (Thomson *et al.* 1996); this method should simply be considered a descriptive approach to delineating the upper edge of the point distribution. However, if the effect of neighbours is just one factor of many influencing the experimental targets, then using the upper boundary would be a refinement of the standard regression technique and would better describe per-gram competitive effects.

I tested differences in total competitive effect among neighbour species using analysis of variance, and tested differences in per-gram effect and per-gram boundary effect by comparing the 95% confidence intervals (CI) of the values of c among target species. I used the Spearman rank correlation (r_s) to compare rankings in total and per-gram competitive ability to rank in natural abundance. Natural abundance is based on the frequency of occurrence of species in 193 plots from a 1996 survey of the same field (see Howard 1998).

GARDEN EXPERIMENT

I established the garden experiment in a cleared and levelled site of the Edwin S. George Reserve. An area approximately 30×21 m was tilled to a depth greater

than 20 cm and a 2-m high deer fence was erected around the site to exclude large herbivores.

The experiment incorporated a pairwise matrix of all possible target-neighbour combinations of seven target species and six neighbour species. Four of the neighbour species from the field experiment (*Centaurea*, *Chrysanthemum*, *Hieracium*, *Poa*) were used as targets, plus *Achillea millefolium* L., *Hypericum perforatum* L., and *Rumex acetosella* L. All target species except *Rumex* were used as neighbours.

Seeds of all species, collected on-site in previous years, were germinated in a glasshouse from 27 April to 2 May 1994, with the timing of sowing varied among species in order to equalize emergence. Between 9 June and 19 June, seedlings ($n = 2520$) were planted in 60 fan-design arrays (two each for 18 of the 42 target-neighbour combinations, one each for the remainder). The arrays utilized an additive design of eight densities arranged in modified hexagonal fans that efficiently used neighbour individuals. Each target was planted in the middle of six neighbours that encircled the target in the form of a hexagon. Eight connected hexagons formed a fan of eight neighbour densities (see Antonovics & Fowler 1985 and Kunin 1993 for a discussion of hexagonal fan arrays and geometry).

While each target-neighbour combination had eight densities, these densities were restricted to only one or two localities (one or two fans) and not randomly dispersed throughout the block. Thus comparisons at the individual species level for both targets and neighbours (a two-way ANOVA of target and neighbour main effects and their interactions) are autocorrelated and violate the assumption of independence. Instead, I combined all targets for each neighbour species to obtain a mean effect competitive ability that could be statistically compared among neighbour species.

Between 23 September and 17 October 1994, I harvested the root and shoot biomass of all living targets in all fans. I harvested neighbour roots and shoots in 14 fans and only neighbour shoots in the remaining 46 fans. Roots were washed free of soil while shoots were harvested by clipping at ground level. Individuals were dried at 60 °C and weighed to the nearest 0.001 g.

Analysis

To assess the magnitude of per-gram neighbour effect, I fitted the reciprocal-yield equation (eqn 2) to target final size vs. an index of neighbour standing crop. I standardized target performance to the largest target plant in each fan, then merged all targets under each neighbour species for the analysis of neighbour effect. The index of neighbour standing crop was based on the size of each neighbour and its distance to the target:

$$N = \Sigma_{i \to n} (a_i / D_i^2)$$

where N is the standing crop index, a is neighbour biomass, D is the distance of the neighbour to the target, and each i represents each neighbour harvested in the hexagon surrounding the target. The results were unchanged when neighbours outside the immediate hexagon were included in estimates of N. I fitted the reciprocal yield equation using the methods described for the field experiment. For the boundary analyses, I used three cycles of nonlinear regression to estimate the boundary instead of two cycles as in the field experiment.

I also estimated the total competitive effects of the four densest neighbourhoods in each fan on targets with RII (eqn 1), where T_{-N} represents the target in the largest (least dense) hexagon. If the target from the largest hexagon died, the fan was excluded from the analysis.

To assess differences in competitive effect among neighbour species, I compared: (i) values of RII among neighbour species using ANOVA, and compared the competition coefficients from the reciprocal-yield equation using 95% confidence intervals; (ii) rankings in competitive ability pairwise with ranks in natural abundance, as in the previous experiment; and (iii) > 2 rankings at a time among both experiments with Kendall's coefficient of concordance, W (Sokal & Rohlf 1995).

Table 3 The magnitude of neighbour effect on *Centaurea* and *Hieracium* (combined, see text) target performance and the associated rankings of competitive effect for the five neighbour species in the field. Relative interaction intensity (RII), ignores neighbour density but provides an easily ascertained index; per-gram effects are reflected in a value (*c*) that represents the shape of a nonlinear curve (either fitted normally or with a boundary procedure, see text). Each ranking is compared to natural abundance using the Spearman rank correlation (r_s)

Neighbour	Total effect		Per-gram effect		Per-gram boundary effect		
	Mean RII	Rank	*c*	Rank	*c*	Rank	Abundance rank
Poa	−0.152	4	0.988	1	0.182	2	1
Centaurea	−0.522	2	0.295	3	0.101	3	2
Hieracium	−0.727	1	0.836	2	0.240	1	3
Danthonia	−0.477	3	0.234	5	0.089	4	4
Chrysanthemum	−0.035	5	0.264	4	0.067	5	5
r_s	0.30		0.80†		0.70		

†$P = 0.1$.

Results

FIELD EXPERIMENT

Total competitive effects of neighbours were all negative, indicating a competitive effect of neighbour presence in all target-neighbour combinations (Table 3). Analysis of variance reveals significant target ($P < 0.05$) and neighbour ($P < 0.01$) effects with no interaction between them. Thus, neighbours differ in their total competitive effect, indicating the presence of this type of competitive hierarchy. The lack of interaction indicates that the rankings of total effects of neighbours do not differ between target species and data for *Centaurea* and *Hieracium* targets can therefore be combined to compare overall effects of each neighbour species. *Hieracium* neighbours had the strongest total competitive effect on *Centaurea* and *Hieracium* targets combined, followed closely by *Centaurea* and *Danthonia* (Table 3). *Poa* and *Chrysanthemum* had the least total competitive effect. Rank in total competitive effect, however, was poorly correlated with rank in abundance ($r_s = 0.30$; Table 3).

Positive values for *c* indicate a per-gram competitive effect of neighbours in all cases and a relatively high r_s value (0.80, Table 3) suggests a significant ($P < 0.1$) relationship between per-gram competitive effect and abundance. *Poa* and *Hieracium* clearly had the strongest per-gram competitive effect, and *Chrysanthemum* and *Danthonia* the least (Table 3, Fig. 1). The fitting procedure generated wide 95% confidence intervals resulting in few significant differences in values of *c* among neighbour species.

Estimates of per-gram competitive effect based on the boundary analyses show a relatively strong correlation with rank in abundance ($r_s = 0.70$). Although species within pairs were reversed, *Hieracium* and *Poa* again had the strongest per-gram competitive effect, while *Danthonia* and *Chrysanthemum* had the least per-gram effect (Table 3).

GARDEN EXPERIMENT

All interactions in the garden experiment were strongly competitive (Table 4, Fig. 2). All comparisons using total (root + shoot) mass of targets were very similar to those using shoot biomass and shoot-only data are presented to allow better comparison with the field experiment.

Neighbour species differed significantly in RII ($P < 0.01$), indicating a strong hierarchy in total competitive effect. *Centaurea* had the strongest total competitive effect and *Hypericum* the least (Table 4). As in the field experiment, the Spearman-rank correlation between rank in total competitive effect and rank in natural abundance was relatively low ($r_s = 0.429$), suggesting little influence of total competitive effect on abundance.

The rankings of per-gram competitive effects were similarly poorly correlated with natural abundance, mainly as a result of the abundant *Centaurea* being the
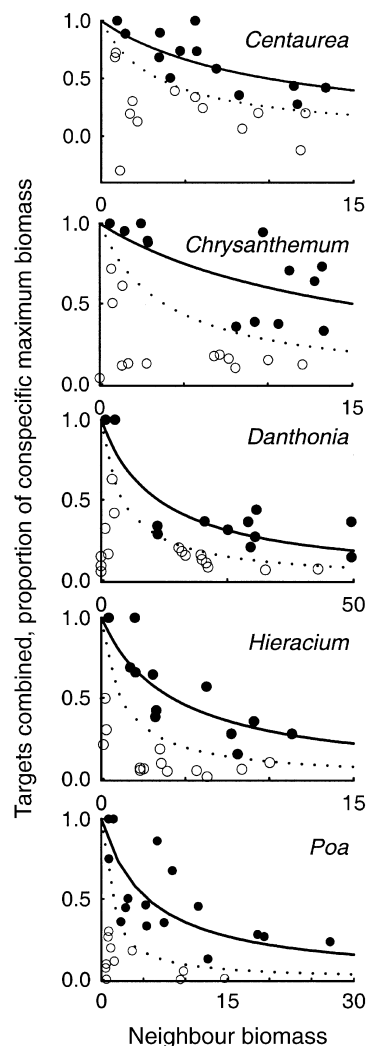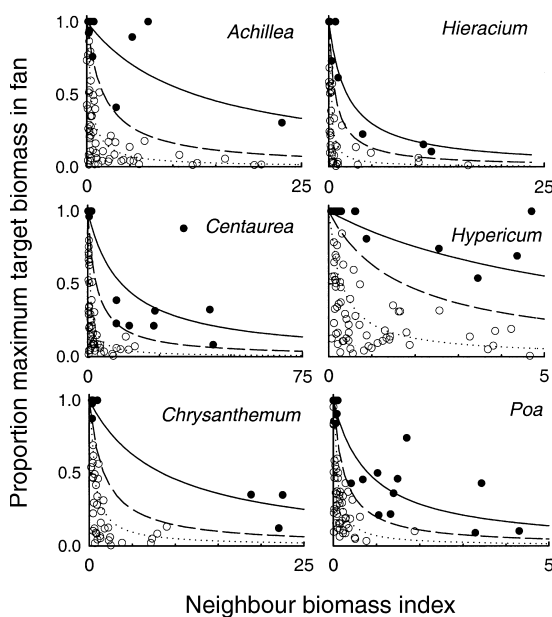
Fig. 1 Proportion of maximum target performance (*Hieracium* and *Centaurea* combined) as a function of above-ground neighbour biomass (g m^{-2}) for all five neighbour species in the field experiment. Each plot shows a two cycle boundary analysis with the dotted line indicating the first cycle (the fit to all of the data), and the solid line indicating the second cycle (the fit to the positive residuals of the first fit). Open circles have negative residuals to the first fitted line, closed circles have positive residuals. The fitting procedure fixes the intercept at one and fits only the shape of the curve (see also Table 3).

worst competitor according to this measure. Although *Poa*, *Hieracium* and *Hypericum* continued to have larger per-gram competitive effects than *Centaurea*, *Chrysanthemum* and *Achillea* when calculated from the upper boundary of points, there was now a strong correlation with natural abundance ($r_s = 0.829$, Table 4). For both types of per-gram analyses, the 95% confidence intervals for the values of *c* generally overlap with adjacently ranked values but not with values at opposite ends of the rankings.

Four species (*Poa*, *Centaurea*, *Hieracium*, and *Chrysanthemum*) were used in both experiments, allowing the rankings of these species to be compared between experiments. The four rankings from the two experiments that are based on per-gram competitive effect are highly correlated with each other ($W = 0.850$,

Table 4 Competitive effect rankings for shoot biomass in the garden experiment and comparisons to natural abundance. Tests are similar to those in Table 3

Neighbour	Total effect		Per-gram effect		Per-gram boundary effect		
	Mean RII	Rank	c	Rank	c	Rank	Abundance rank
Poa	−0.725	4	32.722	1	2.908	1	1
Centaurea	−0.836	1	2.620	6	0.178	4	2
Hieracium	−0.770	2	9.676	3	0.860	2	3
Hypericum	−0.529	6	17.015	2	0.776	3	4
Chrysanthemum	−0.764	3	3.427	5	0.143	5	5
Achillea	−0.699	5	4.633	4	0.094	6	6
r_s	0.429		0.314		0.829*		

*$P < 0.05$.

Fig. 2 Proportion of maximum target shoot performance as a function of the neighbour biomass index for six neighbour species in the garden experiment. Each plot shows a three cycle boundary analysis with the dotted line indicating the first cycle (the fit to all of the data), the dashed line indicating the second cycle (fitting the positive residuals from the first fit), and the solid line indicating the third cycle (fitting the positive residuals of the second fit). Open circles have negative residuals to the second fitted line, closed circles have positive residuals (see also Table 4).

$P = 0.017$), and adding the ranking based on abundance decreases the correlation slightly but increases its significance ($W = 0.776$, $P = 0.009$). However, adding the two rankings based on total competitive effect dramatically decreases both the level of concordance and power ($W = 0.467$, $P = 0.038$; $W = 0.461$, $P = 0.021$, with and without abundance, respectively).

Discussion

The most striking of these results is the suggestion that small differences in per-gram competitive effects may provide a better prediction than total competitive effects

of community-level performance. This is indicated by stronger correlation with rank abundance (Tables 3 & 4), and by the higher levels of concordance in rank across experiments.

Total competitive effect based on RII or any other index from additive design experiments (e.g. RCI, 'absolute competitive intensity' and 'competitive intensity', see Grace 1995) most closely reflects size differences among neighbours (Gaudet & Keddy 1988, 1995). Differential per-unit uptake of resources would certainly be a major component of total competitive effect if species were equal in size, but in reality size differences among species tend to increase and this rapidly becomes the dominant factor influencing resource uptake. Final neighbour sizes did differ in both experiments (reflected in total biomass, Table 1), and while there is no direct relationship between neighbour size and RII, the influence of neighbour size on RII is evident at least for *Achillea*, *Hieracium* and *Hypericum* in the garden experiment (Fig. 3).

The magnitude of the per-gram effect may be interpreted biologically as indicating how rapidly suppression would increase if neighbour size were to increase. The per-gram competitive effect of a species can be applied at a range of neighbour sizes, for example, to predict the magnitude of effect at any other neighbour mass. The nonlinear effects of neighbours on target performance (Watkinson 1980; Weiner 1982), mean that estimates of total effect can, in contrast, provide little information about competitive effects at other neighbour densities. Thus, while estimates of total competitive effects reflect only current conditions, per-gram effects may predict how the influence of neighbours will change over time. Species with low per-gram competitive effect will increase less rapidly in total competitive effect over time than those with a high per-gram effect. Over time, the long-term outcome of competition (*sensu* Welden & Slauson 1986; Gibson *et al.* 1999) may, therefore, be expected to be more related to per-gram competitive effects than to total competitive effects.

A second explanation for the results may be the longer duration of relevant per-gram than total effects between two competing individuals. For example, higher per-gram competitive ability may be a reflection of greater per-unit
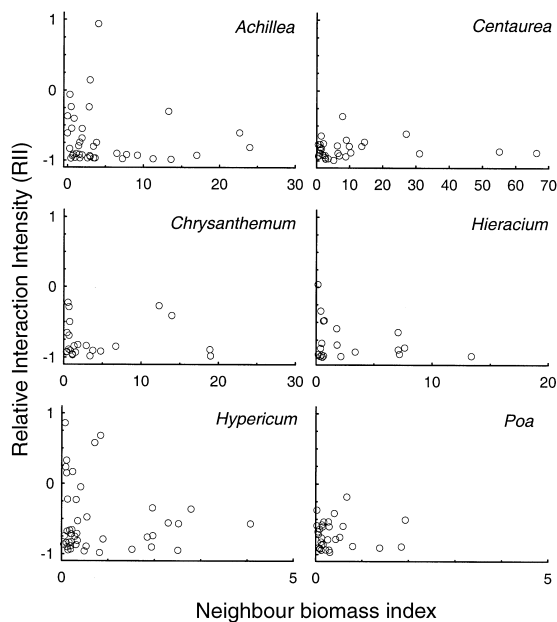
Fig. 3 Relative interaction intensity (RII) for above-ground target biomass vs. *N* (the index for neighbour biomass) for each neighbour species in the garden experiment. Values for RII are calculated from the four highest densities for each experimental fan in comparison to the lowest density target in the fan. A boundary for a negative relationship is evident in *Achillea*, *Hieracium* and *Hypericum*, while not as strongly evident for the remaining species.

nutrient acquisition rates in roots. Models show that slight changes in resource depletion rates can alter competitive outcomes (Huston & Smith 1987; Berendse & Elberse 1990; Pacala *et al.* 1993) and suggest that the small differences in per-gram competitive effect may have significant biological effects on the structure of a plant community. Size-based competitive effects only become relevant when an individual is larger than its competitors, but good per-gram competitors will always acquire more resources relative to their size than their neighbours. This would benefit the individual throughout its life span, rather than only at later stages in life, providing the individual with cumulative benefits that may outweigh the shorter-term benefits of size.

SIMILARITIES AND DIFFERENCES AMONG EXPERIMENTS

Competitive effects were widespread in both experiments: all species showed a mean reduction in size of 72% in the presence of neighbours in the garden experiment and an average of 38% in the field experiment. The less intense suppression in the field is probably a result of lower neighbour densities, but the two experiments cannot be regarded as located at different points along a gradient of competitive effect based on neighbour standing crop. An environmental gradient of resource supply is also apparent, as maximum target size in the two experiments differed considerably; *Centaurea* targets with no neighbours in the field had a mean weight of 0.544 g compared with 23.64 g at low neighbour

density in the garden experiment (equivalent values for *Hieracium* were 0.799 and 5.05 g, respectively). These differences are even more striking as the targets were planted as seedlings in the garden experiment and adults in the field, suggesting that different abiotic conditions were likely to have been important.

Differences in abiotic conditions among experiments may change the magnitude of competitive effects among species (Campbell & Grime 1992; Turkington *et al.* 1993) and thus add variation to the rankings of total and per-gram competitive effect. Yet despite the fact that the experiments differed in so many ways (abiotic conditions, life-history stage, neighbour densities), rankings of RII between experiments are relatively highly correlated ($r_s = 0.600$). This, together with the high correlation of per-gram competitive effects among experiments, suggests that although differences in total and per-gram competitive effect may be slight among species of similar habits and functional groups, those differences that can be detected may be consistent among experiments and within each method of estimating competitive effect, but not between these methods.

In summary, this study is the first to compare species rankings based on both total competitive effect and per-gram competitive effect. In both experiments, total competitive effects differed significantly among species but offered poor prediction of natural abundance, whereas rankings based on per-gram competitive effect were generally more correlated with natural abundance even though differences among species were very small. Estimating per-gram effects using the upper boundary of the point distribution may further refine rankings of per-gram competitive effects. Per-gram competitive effects may be more relevant in estimating natural abundance of species in similar functional groups because of the longer term advantage of the assumed higher rates in per-unit resource uptake.

Acknowledgements

References

Antonovics, J. & Fowler, N.L. (1985) Analysis of frequency and density effects on growth in mixtures of *Salvia splendens* and *Linum grandiflorum* using hexagonal fan designs. *Journal of Ecology*, **73**, 219–234.

Berendse, F. & Elberse, W.Th. (1990) Competition and nutrient availability in heathland and grassland ecosystems. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 93–116. Academic Press, London.

Callaway, R. (1995) Positive interactions among plants. *Botanical Review*, **61**, 306–349.

Campbell, B.D. & Grime, J.P. (1992) An experimental test of plant strategy theory. *Ecology*, **73**, 15–29.

Casper, B.B. & Jackson, R.B. (1997) Plant competition underground. *Annual Review of Ecology and Systematics*, **28**, 545–570.

Chapin, F.S.I. (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.

Connolly, J. (1986) On difficulties with replacement-series methodology in mixture experiments. *Journal of Applied Ecology*, **23**, 125–137.

Connolly, J. (1997) Substitutive experiments and the evidence for competitive hierarchies in plant communities. *Oikos*, **80**, 179–182.

Firbank, L.G. & Watkinson, A.R. (1987) On the analysis of competition at the level of the individual plant. *Oecologia*, **71**, 308–317.

Fowler, N.L. (1990) The effects of competition and environmental heterogeneity on three coexisting grasses. *Journal of Ecology*, **78**, 398–402.

Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.

Gaudet, C.L. & Keddy, P.A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology*, **76**, 280–291.

Gibson, D.J., Connolly, J., Hartnett, D.C. & Weidenhamer, J.D. (1999) Designs for greenhouse studies of interactions between plants. *Journal of Ecology*, **87**, 1–16.

Goldberg, D.E. (1987) Neighborhood competition in an old-field plant community. *Ecology*, **68**, 1211–1223.

Goldberg, D.E. (1996) Simplifying the study of competition at the individual plant level: consequences of distinguishing between competitive effect and response for forest vegetation management. *New Zealand Journal of Forestry Science*, **26**, 19–38.

Goldberg, D.E. & Fleetwood, L. (1987) Competitive effect and response in four annual plants. *Journal of Ecology*, **75**, 1131–1144.

Goldberg, D.E. & Landa, K. (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013–1030.

Goldberg, D.E. & Werner, P.A. (1983) Equivalence of competitors in plant communities: a null hypothesis and a field approach. *American Journal of Botany*, **70**, 1098–1104.

Gordon, D.R., Welker, J.M., Menke, J.W. & Rice, K.J. (1989) Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia*, **79**, 533–541.

Grace, J.B. (1995) On the measurement of plant competition intensity. *Ecology*, **76**, 305–308.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological theory. *The American Naturalist*, **111**, 1169–1194.

Howard, T.G. (1998) *The relationship of competitive hierarchies for germination, growth, and survivorship to relative abundance in an old field community*. PhD Dissertation. University of Michigan, Ann Arbor, MI.

Howard, T.G. & Goldberg, D.E. (in press) Competitive response hierarchies for germination, growth, and survival and their relative influence on abundance in an old field community. *Ecology*, **82** (4).

Huston, M. & Smith, T. (1987) Plant succession: life history and competition. *The American Naturalist*, **130**, 168–198.

Hutchinson, G.E. (1957) Concluding Remarks. Population Studies. Animal Ecology and Demography. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

Jolliffe, P.A. (2000) The replacement series. *Journal of Ecology*, **88**, 371–385.

Keddy, P.A., Twolan-Strutt, L. & Wisheu, I.C. (1994) Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? *Journal of Ecology*, **82**, 635–643.

Kohyama, T. (1992) Size-structured multi-species model of rain forest trees. *Functional Ecology*, **6**, 206–212.

Kunin, W.E. (1993) Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology*, **74**, 2145–2160.

Markham, J.H. & Chanway, C.P. (1996) Measuring plant neighbor effects. *Functional Ecology*, **10**, 548–549.

Miller, T.E. & Werner, P.A. (1987) Competitive effects and responses between plant species in a first-year old-field community. *Ecology*, **68**, 1201–1210.

Pacala, S.W., Canham, C.D. & Silander, J.A. Jr (1993) Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Canadian Journal of Forest Research*, **23**, 1980–1988.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: the Principles and Practice of Statistics in Biological Research*. 3rd edn. W.H. Freeman, New York, NY.

Suding, K.N. & Goldberg, D.E. (1999) Variation in the effects of vegetation and litter on recruitment across productivity gradients. *Journal of Ecology*, **87**, 436–449.

Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S. & Legendre, P. (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology*, **77**, 1698–1715.

Tilman, D. (1977) Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology*, **58**, 338–348.

Tilman, D. (1980) Resources: a graphical-mechanistic approach to competition and predation. *The American Naturalist*, **116**, 362–393.

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

Watkinson, A.R. (1980) Density-dependence in single-species populations of plants. *Journal of Theoretical Biology*, **83**, 345–357.

Weiner, J. (1982) A neighborhood model of annual-plant interference. *Ecology*, **63**, 1237–1241.

Welden, C.W. & Slauson, W.L. (1986) The intensity of competition versus its importance–an overlooked distinction and some implications. *Quarterly Review of Biology*, **61**, 23–44.

Wilson, S.D. (1994) Initial size and the competitive responses of two grasses at two levels of soil nitrogen: a field experiment. *Canadian Journal of Botany*, **72**, 1349–1354.