

# Competitive effect is a linear function of neighbour biomass in experimental populations of *Kochia scoparia*

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## Summary

**1** Neighbour size and distance are confounded in most studies of plant growth and competition at the individual level. To investigate the effects of neighbour size on competitive effect, we grew target *Kochia scoparia* individuals surrounded by six equidistant, even-aged conspecific neighbours. We varied neighbour size by sowing groups of neighbours at different times, and we also varied the sowing time of the target plants to generate variation in both neighbour and target size during the process of competition. We analysed the growth of target plants over two time intervals as a function of their own size and the size of their neighbours at the beginning of the interval.

**2** When competition became intense, the relative growth rate of target plants was primarily determined by the size of their neighbours. There was a negative linear relationship between the relative growth rate of target plants over an interval and the biomass of their neighbours at the beginning of the interval. The size of the target plant itself did not make a significant additional contribution to predicting its growth rate. There is a limit on the growth in biomass of the population (target + neighbours), and growth of individuals occurs within this constraint. Local biomass density, which can be primarily determined by neighbouring individuals, can be much more important for an individual's growth than its own size.

**3** There was no evidence of size-asymmetric competition. The size of neighbours was the primary determinant of a target plant's relative growth rate, but the effect of a given amount of neighbour biomass was the same for neighbours larger and those smaller than the target plant.

*Key-words:* local crowding, local density, neighbourhood competition, neighbour size, plant competition, size-symmetric competition, target plant

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## Introduction

We have a quantitative understanding of plant competition only at the population level. Density–yield relationships, such as the ‘law of constant final yield’ and patterns of self-thinning, have been successfully modelled by researchers (Silvertown & Charlesworth 2001). One of the primary goals of population ecology is to explain population phenomena in terms of the behaviour of individuals. Foresters and plant ecologists have made numerous attempts to model the performance (e.g. size, growth or reproductive output) of individual ‘target’ plants as a function of measures of local crowding

(Stoll & Weiner 2000) such as the number, distances and sizes of neighbouring trees (Aaltonen 1926; Opie 1968; Bella 1971; Weiner 1984; Woodall *et al.* 2003; D’Amato & Puettmann 2004). A complete description of an individual plant’s competitive environment would include the number, size, distance, genotype and angular dispersion of all its neighbours (Mack & Harper 1977). Most studies have looked at only a small subset of these factors. While there have been some limited successes, attempts to account for target plant performance as a function of measures of local competition have been frustrated by several obstacles, which are briefly discussed below.

Static (‘snapshot’) description of neighbour relationships (e.g. Goldberg 1987) can make only a limited

contribution to our understanding of competition among individual plants. Showing, for example, that larger individuals within a crowded population tend to have small neighbours, while relatively small individuals tend to have large neighbours, is not very informative, as plant size and neighbour size are not independent in any sense (Mitchell-Olds 1987). It is not clear if large individuals are large because they have small neighbours, or if the neighbours are small because their neighbour, the target plant, is large. All such a static relationship shows is that the total biomass of target + neighbours is limited, i.e. competition is occurring. To contribute to our understanding of the dynamics of competition, models of local competition need to be dynamic, looking at changes in target plant behaviour as a function of neighbourhood conditions at the beginning of one or more growth intervals.

The simplest dynamic models look at the size or reproductive output of an individual plant as a function of the number of neighbours within a given radius ('neighbourhood distance') from the subject individual (e.g. Silander & Pacala 1985). If there has been no density-dependent mortality, then one can argue that the number of individuals around a target plant may be considered independent of the target plant's performance (e.g. Benjamin 1993). The number of individuals within a fixed radius is insufficient information, however, and a whole growing season is too large a time-step, to account for much variation among individuals. There is usually large variation in the sizes of neighbours and therefore their effects. A target tree with 10 small seedlings within 2 m will grow almost unaffected by them, whereas 10 large trees within this distance will certainly have a major effect on the target tree's growth. Also, the effect of a neighbour decays with its distance, and the scale and, perhaps, the form of the decay function changes over the course of plant growth, so it is not surprising that the number of individuals within a fixed distance does not provide much information about the degree of competition experienced by an individual over its life. The relationship between local density and target size is often triangular: plants with many neighbours are almost always small, but plants with few neighbours can be large or small (Goldberg 1987; Stoll & Weiner 2000). We can conclude only that high local density can constrain plant growth. This triangular pattern could occur because factors other than competition limit the performance of many less crowded individuals, but it could also occur because local density is too crude a measure of competition, e.g. some plants have few but large and/or close neighbours.

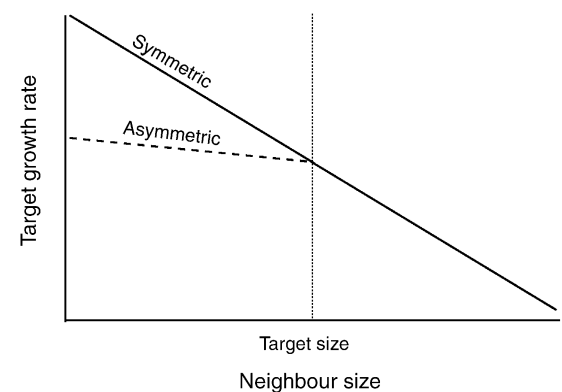
Another complicating factor is the size dependence of plant growth itself. Plant growth during competition can be in large part a function of the plant's size, not just its local competitive environment. Plant growth is sigmoidal (Weiner & Thomas 2001): the relative growth rate decreases, while the absolute growth rate increases and then decreases as a plant grows. Plant size

and neighbour size are often confounded in studies of local competition.

It has rarely been possible to separate the effects of neighbour size from those of neighbour distance, even in experimental studies, because, after a period of growth and competition, these two factors become confounded. For example, if plants are grown at high density, then after a period of growth they will be smaller than if they had been grown at a lower density. Not only is the number of neighbours around an individual target plant higher at higher density, but after competition has started, both the target's size and its neighbours' sizes are smaller than they would be at lower density.

The development of local competition models has also been constrained by the reliance on data from unmanipulated populations in the field. Plants are almost always crowded in nature, and this means that naturally occurring combinations of the different components of local competition, such as neighbour number, size and distance, will be very limited and biased. Experiments that create new combinations of these variables are therefore necessary. To obtain a quantitative understanding of local competition we need to reduce the effects of neighbours to their components, vary these experimentally (Purves & Law 2002), and look at competition over shorter time intervals. A reductionist approach requires that we look at one or a few of these variables at a time, while holding other factors constant. Here we attempt to separate the effects of target and neighbour plant size to study the effects of the latter.

One reasonable hypothesis is that the effect of a neighbour is a function of its size, here defined as above-ground biomass (Goldberg & Werner 1983). Simple 'per-unit-biomass' effects can be used as a null hypothesis in comparing the effects of different species. It can be useful to distinguish the effect of the absolute size of a neighbour from that of its size relative to the target plant. If competition is 'size asymmetric', then we expect the per-unit-size effect of neighbours larger than the target to be greater than for neighbours smaller than the target (Fig. 1). The fit of a local



**Fig. 1** Effect of neighbour biomass on target growth under size-symmetric and asymmetric competition (after Thomas & Weiner 1989).

competition model was significantly improved in two out of three cases when the per-unit-size effects of neighbours smaller than the target plant were discounted (Thomas & Weiner 1989).

We ask the following questions:

1. Is the growth rate of an individual plant experiencing strong competition from neighbours more determined by its own size (size-dependent growth) or by the size of its neighbours (competition)?
2. What is the form of the relationship between neighbour biomass and target plant growth?
3. Is the per-unit-biomass effect of neighbours the same for neighbours larger and smaller than the target plant (size-symmetric competition) or is the effect per unit of biomass greater when neighbours are larger than the target plant (size-asymmetric competition)?

### Materials and methods

We grew *Kochia scoparia* (L.) Schrader, Chenopodiaceae, plants in containers in a glasshouse on top of the Biological Laboratories, Harvard University, Cambridge, Massachusetts, USA, in 32-litre black plastic pots of 33 cm height and a diameter at the top of 37 cm and at the bottom of 33.5 cm. This species was chosen because its biomass can be estimated very accurately from non-destructive, non-invasive measurements such as stem diameter, height and total branch length, and the relationship between these non-destructive measures and biomass is not altered by the competitive environment (Weiner & Fishman 1994; Weiner *et al.* 1997). Seeds were obtained from Thompson and Morgan Co., Jackson, New Jersey, USA.

The pots were filled with pro-mix 'BX', a general-purpose growing medium consisting of 75–85% sphagnum peat moss, perlite, vermiculite, macro- and micronutrients, dolomitic and calcitic limestone and a wetting agent (Premier Horticulture Ltd, Red Hill, Pennsylvania, USA). The contents of all bags were mixed prior to filling the pots in order to reduce potential heterogeneity.

Seeding of germination trays started on 17 February 1995 and was performed over several days to generate size variation for target and neighbour plants. After reaching a height of about 3 cm plants were transplanted to 1-L pots to await transplantation into the final positions in the larger pots on 27 March.

Target plants were surrounded by six even-sized neighbours at a distance of 5 cm from each other and from the target. We varied the size of plants by selecting plants of different ages. Our goal was to generate groups of six even-sized neighbours of five different sizes, and a sixth set with no neighbours. There were six replicates per treatment, giving a total of 36 units. Twenty-four additional units with the same design were used for sequential harvests of each treatment at each of the four measuring times.

We also wanted variation in target plant size for all neighbour sizes, so we deliberately transplanted more

of the older, larger plants into the pots with larger neighbours in an attempt to reduce the confounding of subject plant size and neighbour plant size after a period of growth with competition (see Introduction). Pots were spread out over three benches in the glasshouse to reduce shading by plants in adjacent pots. The position of the pots was re-randomized every second day in order to avoid position effects.

The first measurements were taken on 6 April. From then on, measurements were taken weekly for 4 weeks. For all plants we measured shoot diameter above the cotyledons with digital callipers, and used a ruler to determine the height from cotyledons to the top of the apical meristem and the length of all branches longer than 5 mm. After the last measurement, on 4 May, plants were cut at ground level, dried at 70 °C and weighed. To obtain a robust prediction equation expressing biomass as a function of these measurements, harvesting of spare pots with the same layout was also undertaken during the course of the experiment.

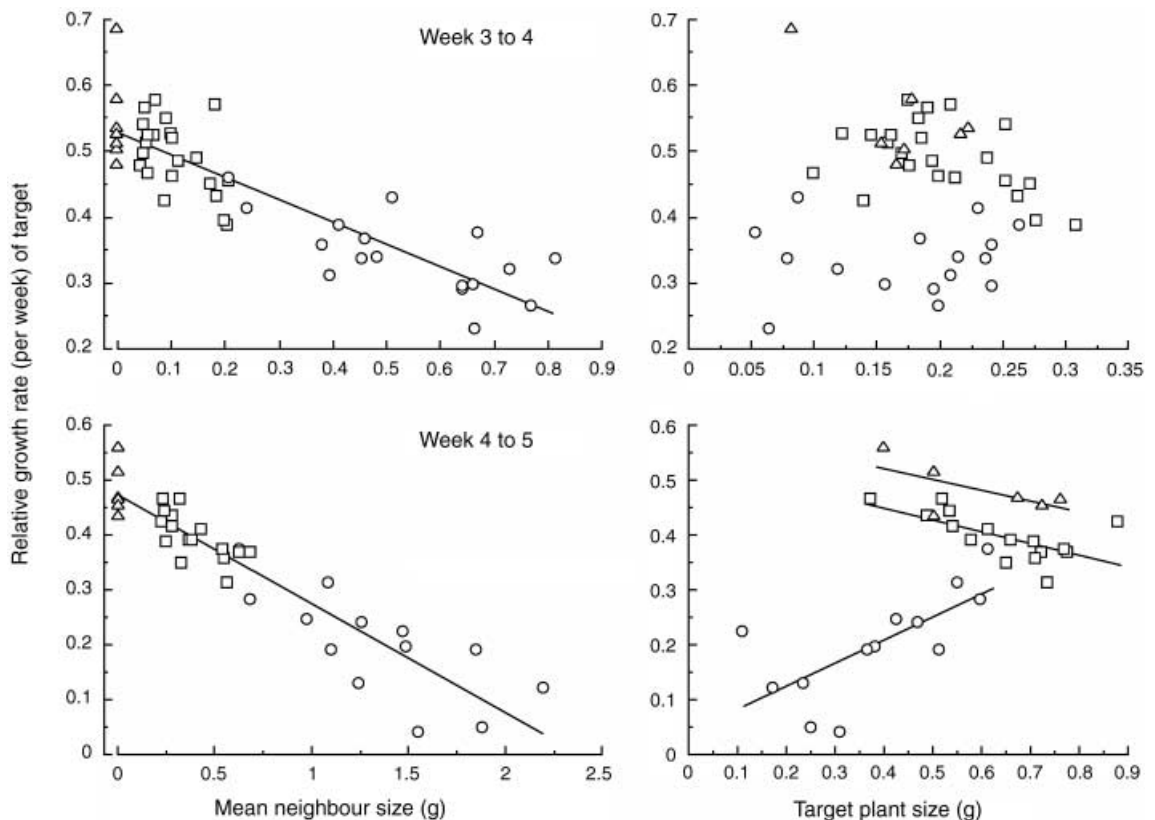
We analysed the relative growth rate in estimated biomass ( $[\log \text{ estimated biomass at time } t + 1] - [\log \text{ estimated biomass at time } t]$ ) of target plants over the last two 1-week intervals as a function of (i) the estimated biomass of the subject plant and (ii) the estimated biomass of its neighbours at the beginning of the interval. We used the relative growth rate (RGR) of target plants as the dependent variable, both because RGR decreases with increasing size over the course of growth, making it easy to investigate at the role of size-dependent growth, and because the distribution of residuals was homogeneous.

### Results

There was a very strong linear relationship between log (stem diameter) and log (dry mass) for all 360 plants harvested ( $r^2 = 0.944$ ). Multiple regression of log mass on log diameter and log (height + total branch length) accounted for 98% of the variation in log mass (log mass =  $-0.992 + 1.401 \log \text{ diameter} + 0.555 \log [\text{height} + \text{total branch length}]$ ). There was no significant difference in the coefficients of this regression for plants between plants used as targets vs. neighbours, and the residuals were homogenous, so we used this equation to predict the biomass of plants over the last 2 weeks of the experiment.

Relative growth rate of targets over the last 2 weeks of the experiment was a linear function of mean neighbour biomass ( $\text{RGR}_{\text{week } 3 \rightarrow \text{week } 4} = 0.530 - 0.341 [\text{mean neighbour size}_{\text{week } 3}], r^2 = 0.745$ ;  $\text{RGR}_{\text{week } 4 \rightarrow \text{week } 5} = 0.473 - 0.198 [\text{mean neighbour size}_{\text{week } 4}], r^2 = 0.858$ ; Fig. 2).

In a general linear model, neither target plant size nor relative neighbour size (larger or smaller than the target), nor interactions, made a significant addition to accounting for variation in target RGR after neighbour biomass was included in the model. Target size alone did not account for significant variation in target



**Fig. 2** Relationship between relative growth rate and (i) mean neighbour size (left side) and (ii) target plant size (right side) from week 3 to week 4 (top) and from week 4 to week 5 (bottom). Triangles = no neighbours; squares = neighbours smaller than target; circles = neighbours larger than target.

RGR in the first period. Target size alone did account for 34% of the variation in the second period, but the relationship between target size and its RGR was very different for plants with larger, smaller or no neighbours. RGR increased with size for plants with larger neighbours, but decreased with size for plants with smaller or no neighbours (Fig. 2). A general linear model with target  $RGR_{\text{week 4} \rightarrow \text{week 5}}$  as the dependent variable, and (a) target size  $\text{week 5}$  and (b) relative neighbour size (neighbours larger, neighbours smaller, no neighbours) and their interaction ( $a \times b$ ; Fig. 2, lower right) accounted for almost 84% of the variation in RGR. Neighbour biomass alone still performed better as a predictor of target growth.

We tried regressions using numerous measures based on relative neighbour size (neighbour biomass/target biomass), but all performed much more poorly than simple neighbour biomass.

## Discussion

As competition became intense during the last 2 weeks of the experiment, neighbour biomass was the primary determinant of target RGR. Target size did not make an additional contribution to accounting for variation in target RGR. A simple explanation for this is that the biomass production by the group of seven plants, the

target plus six neighbours, is constrained. The six neighbours contribute more to this constraint than the single target. Even though we used relatively large containers and inspection of the roots afterwards suggests that the plants were not pot-bound, the simplicity of the results could be due to the limited soil volume in the containers. Purves & Law (2002) found the effect of neighbours to be proportional to the log of neighbour size in *Arabidopsis thaliana* populations. As they measured size as two-dimensional area and different size dimensions are often related allometrically, our results can be considered generally consistent with theirs.

Among all targets there was no general overall relationship between a plant's RGR and its own size. There were, however, strong relationships between target size and RGR within three groups of targets: those with (i) no neighbours, (ii) neighbours smaller than the target, and (iii) neighbours larger than target, but the relationships were different for each of these groups (Fig. 2). While a model based on target size, neighbour size group and their interaction accounted for almost as much variation as the simple model based on only neighbour size, the simplicity of the latter as well as the higher  $r^2$  argue strongly that it was neighbour biomass that limited target RGR, and that the three different relationships between target size and RGR (Fig. 2, lower right) were a result of this.



Although target plants with larger neighbours were overtopped by their neighbours after 4 weeks, there was no evidence of size-asymmetric competition. The simple linear relationship between target RGR and neighbour size showed no evidence of being different for neighbours larger or smaller than the target. Indeed, targets with no neighbours fit well in the overall relationship (Fig. 2, left). It is possible that size asymmetry would have appeared later as competition became more intense if the experiment had continued.

There are two basic approaches to the study of competition among plants. One approach, used here, is phenomenological/empirical. We model the effects of competition as observed, looking for specific and general relationships. General laws of population behaviour, such as the law of constant final yield and self-thinning relationships, provide important information about plant competitive interactions. The other approach is mechanistic. We would like to explain and predict the effects of plants on one another in terms of mechanisms of competition, especially, but not solely, those mediated by resources (Hikosaka *et al.* 1999; Berntson & Wayne 2000; Hikosaka & Hirose 2001). Bridging the gap between these two approaches and explaining empirical relationships in terms of mechanisms is an important goal for plant ecology. However, because of the complex interactions among the different mechanisms and the dynamics of plant growth, which will change the strength and importance of different mechanisms over time, we are many years away from a mechanistic understanding of plant competition. The bridge between empirical and mechanistic approaches to plant competition must be built from both sides: by developing better mechanistic models, and by increasing our understanding of the empirical patterns that mechanistic models try to explain. In this context it is important to reduce competitive interactions to their constituent components, such as the effects of neighbour size and distance (Purves & Law 2002). If the pattern observed here (i.e. neighbour effect is a simple function of neighbour size) proves to be general, this will have important implications for mechanistic models. If the pattern is not general, then investigating when it holds, and when it does not, will provide important information on the mechanisms of competition among individual plants.

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