2001

Using Upper Boundary Constraints to Quantify Competitive Response of Desert Annuals

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Lessin, L. M., Dyer, A. R. and Goldberg, D. E. 2001. Using upper boundary constraints to quantify competitive response of desert annuals. – Oikos 92: 153–159.

Using a target-neighborhood approach with six annual dicot species in the Negev Desert of Israel, we tested whether neighborhood biomass constrained the upper limit of plant performance and if the slope of the upper boundary was correlated to species trait means, such as relative growth rate (RGR) and seed mass. Target individuals were measured in early spring and then collected at the onset of the dry season along with all naturally occurring neighbors within a 5-cm radius of the target. Using a minimum of 50 samples for each of the six target species, we found no significant relationships between target performance and either density or aboveground biomass of neighbors, when including all target individuals in the regressions. However, aboveground neighbor biomass did influence the maximum potential size of targets. When regressions were restricted to the largest target plant within classes of neighbor biomass, significant negative relationships were found for all six species, with neighbor biomass explaining 55 to 94% of the variance in maximum target biomass. The slopes of the regressions were used as an index of competitive response. The correlations between competitive response and estimates of species traits were not significant with the possible exception that species with lower RGR_{max} may be better response competitors (i.e. were less sensitive to competition). These findings indicate the usefulness of the boundary regression technique for describing competitive interactions among neighbors, particularly in low productivity environments.

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Neighborhood competition in plants often creates an upper limit to performance of individual plants although the exact position below the upper limit is an integration of all environmental factors affecting each plant (Rabinowitz et al. 1985, Firbank and Watkinson 1987, Goldberg 1987, Goldberg and Scheiner 1993, Kaiser et al. 1994, Guo et al. 1998). This phenomenon may be widespread given the large number of biotic and abiotic influences on individual performance under natural conditions (Thomson et al. 1996) and the frequent scatterplot distributions produced by field data (Blackburn et al. 1992, Guo et al. 1998, Scharf et al. 1998). For these target performance vs neighbor abundance distributions, the slope of the upper boundary limit reflects the species performance across a neighbor density or biomass gradient. This value can then be used as a measure of its competitive response, i.e., the ability of an individual to tolerate competition from neighbors (Goldberg and Werner 1983, Goldberg and Landa 1991).

In seasonally productive environments, such as in Mediterranean or desert habitats, annual species must acquire resources and develop rapidly over a relatively short growing season. Under these conditions, if final plant biomass is influenced by competition for resources, then a correlation is predicted between competitive ability and plant characteristics that reflect rapid resource acquisition (Grime 1979, Chapin 1980,

Berendse and Elberse 1990, Lambers and Poorter 1992). Particular traits include those directly related to gathering specific resources (e.g., root traits, specific leaf area) or those that represent an integration of a plant's potential response to the environment (e.g., maximum relative growth rate, maximum final biomass).

In this paper, we first used a boundary regression method to test whether neighborhood competition constrains the upper limit of plant performance in six desert annual species. We then used these regression slopes as a measure of competitive response to test whether competitive response across species was correlated with their maximum plant biomass, growth rate, or several morphological traits. We chose desert annuals because the importance of competition within arid and low productivity systems has been widely discussed, but poorly defined. Indeed, while competition has been postulated as being rare (Noy-Meir 1973) or absent (Grime 1979) in arid systems, numerous studies have reported both positive effects (Muller 1953, McAuliffe 1984, Pugnaire et al. 1996, Holzapfel and Mahall 1999), and negative effects (Fowler 1986, Gurevitch 1986, Kadmon and Shmida 1990, Pantastico-Caldas and Venable 1993) of neighbors on plant growth and survival.

Methods

Study site and species

The study site was a NW-facing slope on a semi-stabilized sand dune at Holot Mashabim Nature Reserve (31.00N, 34.44E) in the Negev desert in Israel where the mean annual precipitation is 110 mm and falls between November and March. The area is characterized by a very diverse annual community with scattered shrubs and bunchgrasses in the *Stipagrostio-Artemisietum monospermae* plant association (Zohary 1982). We chose six commonly occurring dicot species: *Erodium laciniatum* (Cav.) Willd., *Nigella arvensis* L., *Rumex pictus* Forssk., *Senecio glaucus* L., *Lotus halophilus* Boiss. et Spruner, and *Trifolium tomentosum* L. (Table 1). Nomenclature follows Feinbrun-Dothan and Danin (1991).

We established four parallel 50-m transects along a NW-facing dune contour on 10–11 March 1996 and marked a total of 70 individuals of each of the six species with colored toothpicks. Marked plants were no closer than 15 cm to each other to avoid sampling shared neighbors and at least 50 cm from the nearest shrub or bunchgrass to avoid interactions with the perennial species. For each plant, we measured the number of leaves, flower buds and flowers and the length of the longest leaf.

To estimate the initial biomass of the targets, we harvested roots and shoots of 30 specimens of each species adjacent to the transects. A multiple regression of biomass against the size variables was run for each species. Leaf number and the length of the longest leaf were the only significant variables explaining biomass for any of the species. Regression equations using these two variables against total dry mass were used to estimate initial biomass of the target plants in the field (Table 1).

On 6–7 April 1996, a minimum of 50 surviving marked plants of each target species and all surviving neighbors within a 5-cm radius of each target plant were harvested. The shoots of neighboring plants were counted, clipped at ground level, and separated into monocotyledons and dicotyledons. After clipping the neighborhood, we harvested aboveground biomass of each target and as much of the belowground biomass as possible within a 5-cm radius and to a depth of about 15 cm. The size of the neighborhood was chosen to be consistent with previous studies on neighborhood interactions in annual communities.

For each target individual, the number of leaves, flower buds and flowers per plant were counted and the length of longest leaf was measured after which target plants were dried, weighed, and divided into shoots and roots. Shoots were weighed directly and root mass was calculated as the difference between the total and shoot masses. The leaf area of the longest leaf was measured for four of the species, but not for *L. halophilus*, due to the pinnate character of the leaves, or for *R. pictus*, whose leaves fell apart after the size measurements were taken. Dicot and monocot neighborhoods were weighed separately.

Table 1. Characteristics of the six desert annual species in this study. The value for r^2 is from the relationship between plant biomass and both the number of leaves and length of the longest leaf ($n = 30$ except for *L. halophilus* where $n = 29$). Nomenclature follows Feinbrun-Dothan and Danin (1991).

Species	Family	Growth form	r^2	Seed mass (g/100)
Senecio glaucus L.	Asteraceae	erect, height to 20 cm	0.88	0.153
Erodium laciniatum (Cav.) Willd.	Geraniaceae	erect, height to 40 cm	0.98	0.076
Rumex pictus Forssk.	Polygonaceae	rosette, slightly succulent, height to 15 cm	0.90	0.054
Nigella arvensis L.	Ranunculaceae	erect, height <15 cm	0.96	0.049
Lotus halophilus Boiss. et Spruner	Fabaceae	prostrate	0.79	0.042
Trifolium tomentosum L.	Fabaceae	erect, height <15 cm	0.95	0.048

Relative growth rate (RGR) for each target individual was calculated as [(ln (actual final biomass)-ln(estimated initial biomass))/time in days from initial to final measurements] following Grime and Hunt (1975). The greatest observed RGR of each species was considered its RGR_{max}.

For all target individuals of all species, we calculated several morphological traits: the ratio of shoot mass to root mass (S:R); the root length to mass ratio (RLM) was calculated based on the mass of the top 2 cm of the main root; and an estimate of specific leaf area (SLA) based on mass and area of the longest leaf of all species except *L. halophilus* and *R. pictus* (see above). We used the average values of these traits over all individuals to characterize each species and relate to their competitive ability (see below).

Statistical analysis

To compare species of different relative sizes, target individual biomass within a species was standardized by the maximum observed biomass of any target individual of that species. (Note that the largest individual was not necessarily one with no neighbors.) All the regressions described below were run with proportion of maximum target biomass as the dependent variable and neighborhood biomass as the independent variable, and all regressions were given a default intercept of one. This standardization allowed for the comparison of regression lines between species of different absolute sizes.

Upper boundary analysis (Blackburn et al. 1992) uses a subset of the points in a scatterplot in a linear regression to determine whether they represent a constraint on the dependent variable. The x-axis (in this case, neighborhood biomass) is divided into equal width-classes and the highest point within each width class is used in each regression. Although choice of class width is arbitrary, Blackburn et al. (1992) found that fewer than five, or more than twenty, divisions decreased the power of the test. Thus, while the variance explained for target biomass will generally increase using fewer divisions, the number of data points in the regression will decrease.

Because of the potential for biasing the analysis with subjective class widths, we first analyzed a range of widths and compared the results among these classes. For each target species in this study, four regressions were analyzed with neighborhood biomass divisions set at 0.01-g, 0.02-g, 0.025-g, or 0.05-g intervals, which created 40, 20, 16, and 8 potential classes, respectively, along the x axis from which to choose the regression points. Not all classes contained points. The slopes of each regression were used to represent each species' competitive response (Goldberg and Landa 1991) and we used Kendall's concordance test (Sokal

and Rohlf 1981) to compare the rankings of the species competitive response between the different class widths. Significance concordance of ranks would indicate robust results, regardless of class widths.

To assess whether we could explain variation in competitive ability among species by variation in their morphology, we plotted their competitive responses (regression slopes) against species means for seed mass, maximum final target biomass, RGR_{max}, S:R, RLM, and SLA, and constructed a Pearson correlation matrix. Significant correlations are interpreted as evidence of a relationship between competitive ability and the trait.

Results

For all six species, all size and growth measurements (initial biomass estimate, shoot and root biomass, longest leaf length, mass of longest leaf, and RGR_{max}) were positively correlated with final target biomass ($P < 0.01$; exceptions were $P < 0.05$ for one case in *N. arvensis* and two cases for *L. halophilus*, and $P = 0.062$ for one case in *S. glaucus*). Therefore, only final target biomass is used for the analyses presented below; results with other target response variables are similar.

When all data points were included in the regressions, target final biomass was not significantly related to the neighborhood biomass, whether total, of monocots alone, or of dicots alone, and regardless of whether linear, quadratic, or negative exponential regressions were used (in all cases, $P > 0.090$, $r^2 < 0.07$).

In contrast, using the boundary regression technique, linear regressions of the proportion of maximum target biomass against total neighborhood biomass were significant for all six species in at least three of the four selected width classes (Table 2, results for the widest width class are shown in Fig. 1). In nearly all cases, the proportion of variance explained increased, and the significance of the fit decreased, with decreasing number of width classes. At the largest width class (0.05 g), the regression for *S. glaucus* ($n = 4$) and for *R. pictus* ($n = 6$) were not significant at $P < 0.05$, although they did show trends at $P < 0.10$ (Table 2, Fig. 1a, c). All regression slopes were negative. Although the actual slope values depended on width class (slopes were less steep with wider classes), the rankings of competitive response among the species were consistent regardless of width class used for the analysis (Table 2, for all six possible comparisons, Kendall's Tau > 0.600, $r > 0.87$, $P < 0.10$). Species competitive rankings were *N. arvensis* > *T. tomentosum* > *E. laciniatum* > *R. pictus* > *L. halophilus* > *S. glaucus* although the order of *T. tomentosum*, *E. laciniatum*, and *R. pictus* varied in two of the width classes (Table 2).

Table 2. Summary of upper boundary regressions of target final biomass on neighbor biomass for each target species, using the largest target individual from within neighbor biomass classes in each regression. Results are presented from analyses using four different neighbor biomass class widths. Note that with increasing class width, slopes become less negative, r^2 goes up, but P goes down. $+P<0.10$, $*P<0.05$, $**P<0.01$, $***P<0.001$.

Species	Class width = 0.01 g			Class width = 0.02 g			Class width = 0.025 g			Class width = 0.05 g		
	n	r^2	b	n	r^2	b	n	r^2	b	n	r^2	b
S. glaucus	12	0.59	−4.20**	9	0.68	−3.79**	6	0.59	−3.41*	4	0.71	−2.56+
E. laciniatum	20	0.63	−3.37***	12	0.74	−2.39***	9	0.84	−2.24***	6	0.94	−2.05***
R. pictus	19	0.61	−3.46***	12	0.60	−2.71***	10	0.57	−2.47**	6	0.56	−1.84+
N. arvensis	18	0.51	−2.84***	12	0.56	−2.24**	10	0.70	−2.13**	6	0.80	−1.68**
L. halophilus	16	0.68	−3.68***	11	0.79	−3.15***	9	0.82	−2.77***	6	0.89	−2.46**
T. tomentosum	18	0.59	−3.28***	11	0.62	−2.41**	9	0.65	−2.18**	6	0.76	−1.90*

The slopes from the largest width class regressions were used as the estimates of competitive response for correlations with trait means (results are qualitatively identical with slopes using smaller, but more classes). Competitive response was poorly correlated with species maximum biomass, mean seed mass, RLM, SLA, and S:R (Fig. 2, in all cases, $r < 0.60$, $P > 0.08$). Response competitive ability significantly declined with increasing RGR_{max}, but only when *S. glaucus* was omitted as a possible outlier ($P < 0.05$, Fig. 2a).

Discussion

Detecting competitive interactions among annuals in arid and semi-arid environments has met with variable results possibly because the sample populations have not been clearly identified. Many environmental factors result in reduced plant performance. For example, small plants in low density neighborhoods are likely affected by environmental factors other than competition. Therefore, plants showing poor performance for reasons other than neighborhood density confound the quantification of competitive effects.

The boundary regression technique (Blackburn et al. 1992) restricts the analysis to the largest plants in each of several neighbor size classes and thereby includes only those individuals likely to show the influence of competition. In this study, such regressions detected strong negative relationships in all six annual species and support other reports of competitive effects on some aspect of performance in plants of arid habitats (Gurevitch 1986, Kadmon and Shmida 1990, Pantastico-Caldas and Venable 1993, and citations in Fowler 1986).

Despite our poor understanding of resource dynamics and competition in arid environments, analytical techniques such as boundary regression may be useful for detecting underlying relationships and the mechanisms by which they operate (Thomson et al. 1996, Guo et al. 1998). The significant boundary regressions we found at all neighbor biomass width classes indicated that competition may contribute to limitations on plant performance and that it may be possible to assess relative competitive ability based on scatterplots from field data. In addition, the concordance of species competitive hierarchies across all four neighbor biomass width classes, and therefore regression sample sizes, suggests the boundary regression technique was robust despite the high variance in the data for each species.

We used the slope of the boundary regression as an estimate of response competitive ability for each species and these values were concordant across the four neighbor width classes tested. However, correlations between response competitive ability and maximum plant biomass, growth rate, or several morphological measures showed very little evidence of any strong relation-

ships among species. The complex interactions between temporal resource availability, resource variation at the microsite, and the abbreviated desert growing season suggests, with a sample size of six species, a limited ability to detect correlations between plant traits and competitive response to increasing neighbor biomass.

In arid environments, conditions promoting competition may be short-lived and of varying intensity from one year to the next. Goldberg and Novoplansky (1997) suggested that competition may be restricted to the brief periods of seasonal resource availability and would not be characteristic of these habitats throughout the year. Thus, among annual species in desert habitats, the growing season from late winter to early spring is characterized by rapid biomass accumulation and decreasing resource availability, and the necessary conditions for competition are present. However, as spring progresses, the intensifying abiotic conditions and increasing periods between resource pulses increase the probability of mortality and may reduce the importance of competitive interactions in determining final plant biomass.

In this field study, the use of an upper-boundary regression technique revealed that neighbors can limit growth in all six annual species. Although many environmental factors may contribute to the triangular distribution of data, the significant upper-boundary regressions found in target size vs neighbor biomass plots suggest that competition may be one of the factors influencing plant performance in the desert community. These results imply that, while mean resource availability and productivity is low in desert habitats, seasonal resource pulses are sufficient to promote conditions for competition.
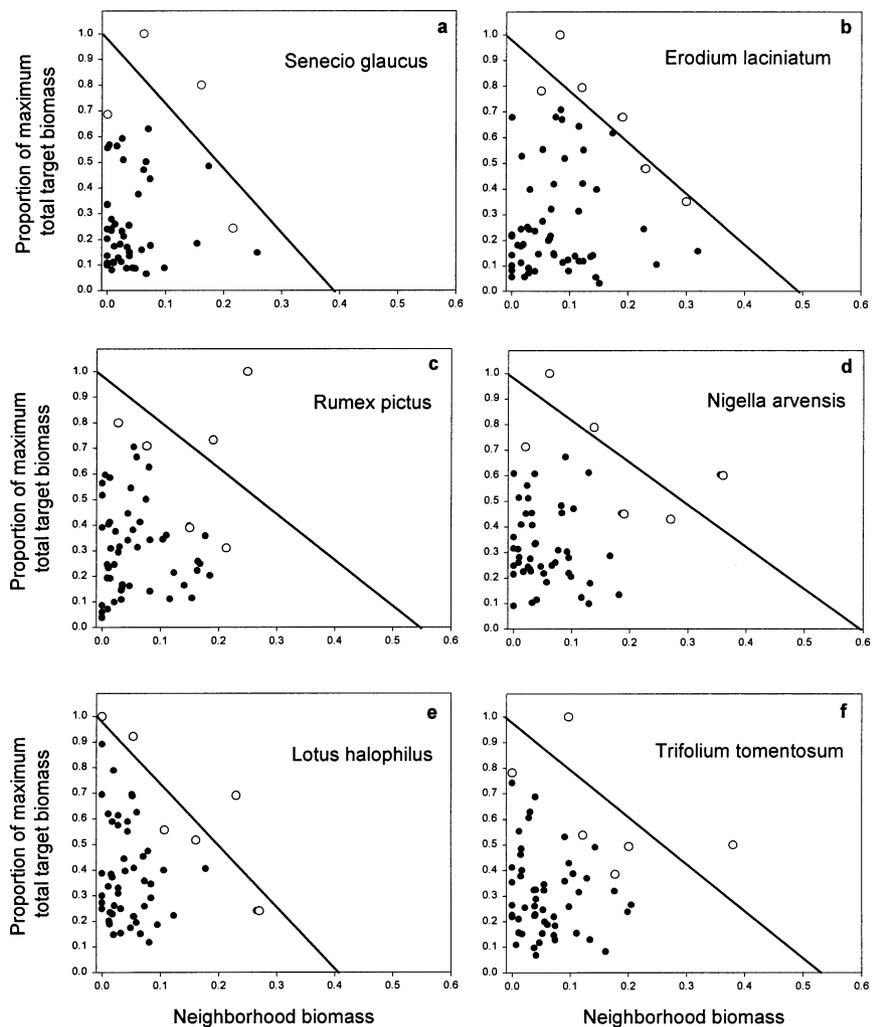
Fig. 1. Plots of the proportion of maximum target mass against total neighborhood mass for six desert annual species (all points). Upper boundary regressions of maximum values in classes 0.05 g wide of neighborhood biomass values (open circles only) are shown with slopes, r^2, and P values. *S. glaucus* and *R. pictus* were marginally significant at this largest neighbor width class (0.05 g), but regressions at all other neighborhood width classes (0.01 g, 0.02 g, 0.025 g) were highly significant for all species (see Table 2). Slopes of regressions (species competitive response) were concordant across neighbor width classes (see text).
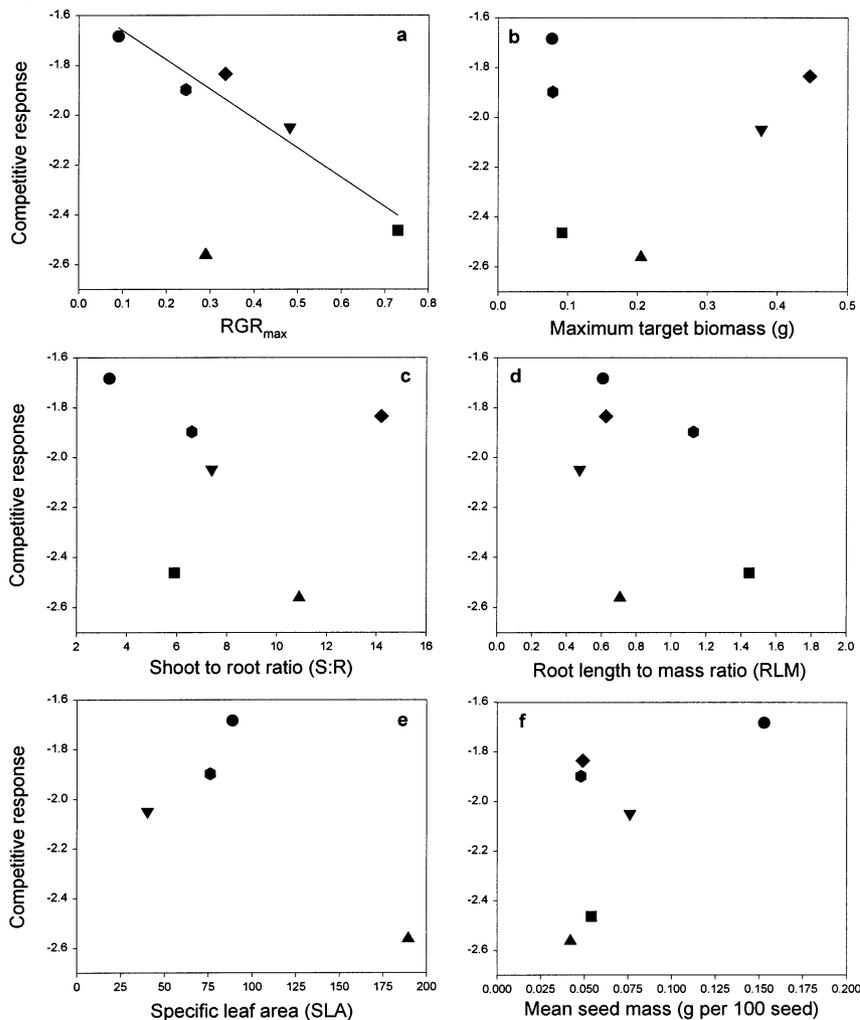
Fig. 2. Correlation plots of species competitive response against species maximum biomass, seed mass, and four morphological trait means. Note that response competitive ability decreases as regression slopes become more negative. Response competitive ability was not significantly correlated with any trait except RGR_{max} when *S. glaucus* was omitted ($r = -0.97$, $P < 0.01$). Note $n = 4$ species for SLA. ● *N. arvensis*, ▼ *E. laciniatum*, ■ *L. halophilus*, ◆ *R. pictus*, ▲ *S. glaucus*, ⬟ *T. tomentosum*.

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