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COMPETITIVE EFFECT AND RESPONSE IN FOUR ANNUAL PLANTS

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SUMMARY

(1) Neighbourhood experiments were used to compare the magnitudes of competitive effect and competitive response using all pairwise combinations of *Papaver rhoeas*, *Triticum aestivum* and *Avena sativa* as neighbour species, and these three species plus *Chenopodium album* as target species.

(2) Over 79% of the variance in target weight was explained by a simple hyperbolic function of neighbour weight or density for seven out of the twelve species combinations.

(3) For all four target species, the two grass neighbour species always had statistically equivalent competitive effects that were generally greater than the effects of *Papaver*. For all three neighbour species, *Papaver* was the weakest competitor in terms of response and *Triticum* was the strongest competitor. With one exception, these hierarchies hold both for effects averaged over all densities of neighbours > 0 and when biomass of neighbours is restricted to a narrow range.

(4) Species that attain larger size when grown with no competition and with larger seeds generally have a greater competitive effect (cause greater reductions in growth of target plants) and a lesser competitive response (growth is reduced less by the presence of neighbours), except that *Chenopodium* is a stronger response competitor than expected from its size with no competition and from its seed size.

(5) Root:shoot ratio of the target plants was significantly affected by the presence of neighbours in nine of the twelve species combinations. The direction of change in relative root allocation was often inconsistent among target species responding to the same neighbour species and among neighbour species affecting the same target species.

INTRODUCTION

Exploitative competitive ability in any organism consists of two distinct aspects: competitive effect, which is the ability of an organism to reduce the performance of other organisms, and competitive response or tolerance, which is the ability of an organism to continue to perform relatively well in the presence of competitors (Goldberg & Werner 1983; Peart & Foin 1985; Miller & Werner 1987). These two aspects of competitive ability are not necessarily correlated in plants: for example, traits that determine the extent to which one plant may shade another are not the same traits that confer tolerance of low light levels. Comparisons of *both* aspects of competitive ability among species are critical for connecting morphological and physiological traits to ability to succeed in a competitive environment.

In this paper we report a series of greenhouse experiments comparing both competitive effects and competitive responses among a group of four species. So that the absolute magnitude of intraspecific competition could be included in the comparisons, we used a form of an additive, rather than the more common substitutive, experimental design

(Harper 1977). In substitutive designs, total density of a two species mixture is held constant and the proportion of each species is varied. Thus, the impact of interspecific competition *relative* to intraspecific competition is measured (de Wit 1960). In additive designs, the density of an indicator or target species is held constant and the density of an associate or neighbour species is varied. The slope of a regression of target performance on competitor density is an index of the absolute magnitude of the *per capita* competitive effect of the competitor species on the target species (Spitters 1983). Alternatively, this same slope can be considered as the response of the target species to an individual of the neighbour species. Additive designs have the additional advantage that non-linearity of *per capita* competitive effects can be quantified. If the target density is reduced to a single individual, the design becomes a neighbourhood experiment and we can measure an additional aspect of the interaction: what proportion of the variance in target individual performance is explained by variation in the amount of neighbours (Mack & Harper 1977; Waller 1981; Weiner 1982, 1984; Liddle, Budd & Hutchings 1982; Fowler 1984; Silander & Pacala 1985; Goldberg 1987). This gives an estimate of the importance of competition in determining the fate of individuals relative to the importance of other factors affecting the plants.

We used neighbourhood experiments to address the following specific questions: (i) How much of the variance in individual performance can be explained by simple functions of the amount of neighbours? (ii) What is the shape of the relationship between target performance and amount of neighbours? (iii) Are the rankings of competitive effect among neighbour species consistent for all target species and are the rankings of response among target species consistent for all neighbour species? That is, are there consistent hierarchies of effect or response? Are the rankings of competitive effect or response, or both, related to seed size or growth rate in the absence of competition? (iv) Are the rankings of competitive effect and competitive response positively correlated? That is, are species that are relatively strong effect-competitors (cause larger reductions in growth or survival) also strong response-competitors (are less affected by the presence of neighbours)?

METHODS

Four annual species were used in all combinations as both targets and neighbours: two grass crop species, *Triticum aestivum* L. (cv. Frankenmuth) and *Avena sativa* L. (cv. Marion), and two weedy dicots, *Chenopodium album* L. and *Papaver rhoeas* L. The two grass species have larger seed weights and, in the absence of competition, attain larger size at final harvest than the two dicot species (Table 1). The seed weights in Table 1 for *Chenopodium* and *Papaver* are from data in Salisbury (1942) and probably are not strictly

TABLE 1. Seed mass ($n = 10$) and mass at final harvest of plants grown for 46 days in pots with no neighbours ($n = 6$). Values are means \pm 95% confidence limits. Seed mass values for *Chenopodium*, and *Papaver* are from Salisbury (1942).

	Seed mass (mg)	Isolated plant mass (g)
<i>Chenopodium</i>	0.65	0.034 \pm 0.051
<i>Papaver</i>	0.14	0.431 \pm 0.139
<i>Triticum</i>	40 \pm 5.7	1.128 \pm 0.393
<i>Avena</i>	34 \pm 7.2	1.647 \pm 0.702

accurate for the seeds used in the experiment. However, an error of fivefold or more would be necessary to change the rankings of seed size among the species. Seeds of both grasses were obtained from commercial seed lots and seeds of the two dicotyledons were obtained from Valley Seed Service in Fresno, California. Because germination of *Chenopodium* was poor, there were too few seedlings to use *Chenopodium* as a neighbour. Thus, there were twelve species combinations: *Chenopodium*, *Papaver*, *Triticum* and *Avena* as targets, and *Papaver*, *Triticum* and *Avena* as neighbours.

For each species combination, there were thirty-six pots, each with one individual of the target species in the centre of the pot and a specified density of the neighbour species. For the grass neighbours, planted densities were 4, 6, 8, 10, 12, 14, 16, 18 or 20 neighbours. Because *Papaver* seeds were much smaller than the grass seeds (Table 1), planted densities of *Papaver* neighbours were twice as high (8–40 plants per pot). There were four replicates of each neighbour density for each species combination. In addition, there were six pots of each target species with a single target individual and no neighbours. These pots were used in the analyses of the effects of all neighbour species on that target.

Pots 15 cm in diameter and 12 cm in depth were filled to within 2.5 cm of the top with a sandy organic potting soil mixture. Seeds of all targets and neighbours were germinated on filter paper and planted at the cotyledon stage. Neighbour seedlings were planted as evenly as possible over the pot and any neighbours that died in the first two weeks after planting were replaced.

To minimize the effect of target individuals on neighbour growth, target individuals were planted 7–9 days after planting of the neighbours. Planting started on 20 January 1983 and took about two weeks to complete.

The pots were arranged randomly on benches in a heated glasshouse at the W. K. Kellogg Biological Station, Michigan, U.S.A. Maximum daytime temperatures ranged from 22 °C at the start of the experiment to 30 °C by harvest. Minimum night temperatures ranged from 14 °C at planting to 17 °C at harvest. In addition to natural light, pots were illuminated by 100-watt cool-white fluorescent tubes to extend the photoperiod to 14 hours. All pots were watered for ten minutes daily with a fine misting system. Half-way through the experiment (twenty-three days after planting) a commercial fertilizer (Miracle-gro) was added to all pots. Pots with grass neighbours were staked and wrapped with twine to prevent lodging.

Each pot was harvested forty-six days after planting of target individuals. Soil was washed from the roots under gently running water. Target individuals were separated from neighbours and then both targets and neighbours were separated into above- and below-ground components. Plant parts were placed in a plant press, dried for 48 hours at 65 °C and weighed.

All analyses were performed with the BMDP statistical program (Dixon 1983).

RESULTS

There are strong, usually non-linear competitive effects of increasing neighbour density or biomass on target size at harvest for all species combinations, except *Papaver* neighbours on the two grass targets (Figs 1 and 2). Of several functions fitted to the data (linear, power, exponential, hyperbolic), the best fit was a hyperbolic model, $T = T_{\max}/(1 + xN)$, derived from the reciprocal yield model for intraspecific density dependence (Weiner 1982), where T is total target weight, N is total neighbour weight or density, and x and T_{\max} are fitted constants. The R^2 values from the hyperbolic functions were extremely high

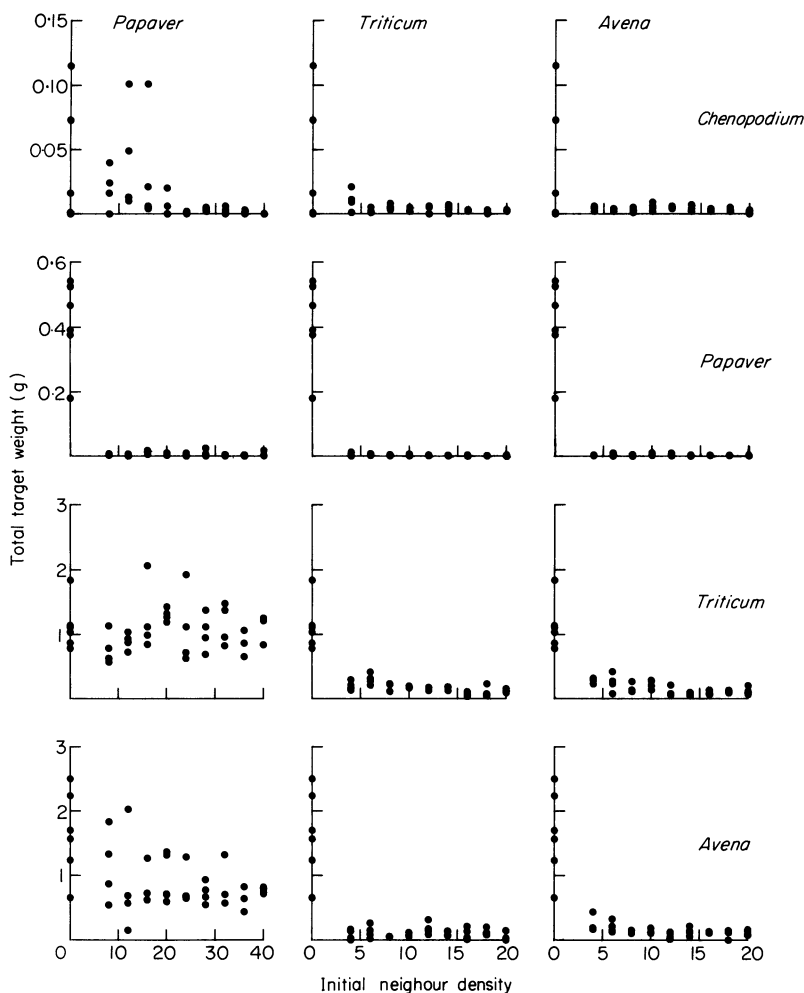


FIG. 1. Relationship between total target weight and neighbour density for twelve combinations of target and neighbour species. Names of the three neighbour species are listed across the top and of the four target species along the right side.

(> 0.79) for seven of the twelve species combinations, much weaker for all competitive effects on *Chenopodium* targets and usually very small for the effects of *Papaver* on the two grass targets (Table 2). The proportion of variance in target weight explained by neighbour density and neighbour weight were generally similar (Table 2). In all regressions, the values for x were positive, indicating competitive effects.

The high R^2 values and the strongly curvilinear relationship in Figs 1 and 2 are largely due to the difference between having no neighbours and having any neighbours at all. If the pots with no neighbours are excluded, the relationships are generally described better by a linear model than by the non-linear models and the R^2 values are all much smaller (Table 3). Furthermore, a number of the relationships are actually positive (Table 3). The small proportion of variance in target weight explained by neighbours for densities greater than 0 suggests that there was little or no difference in target performance among

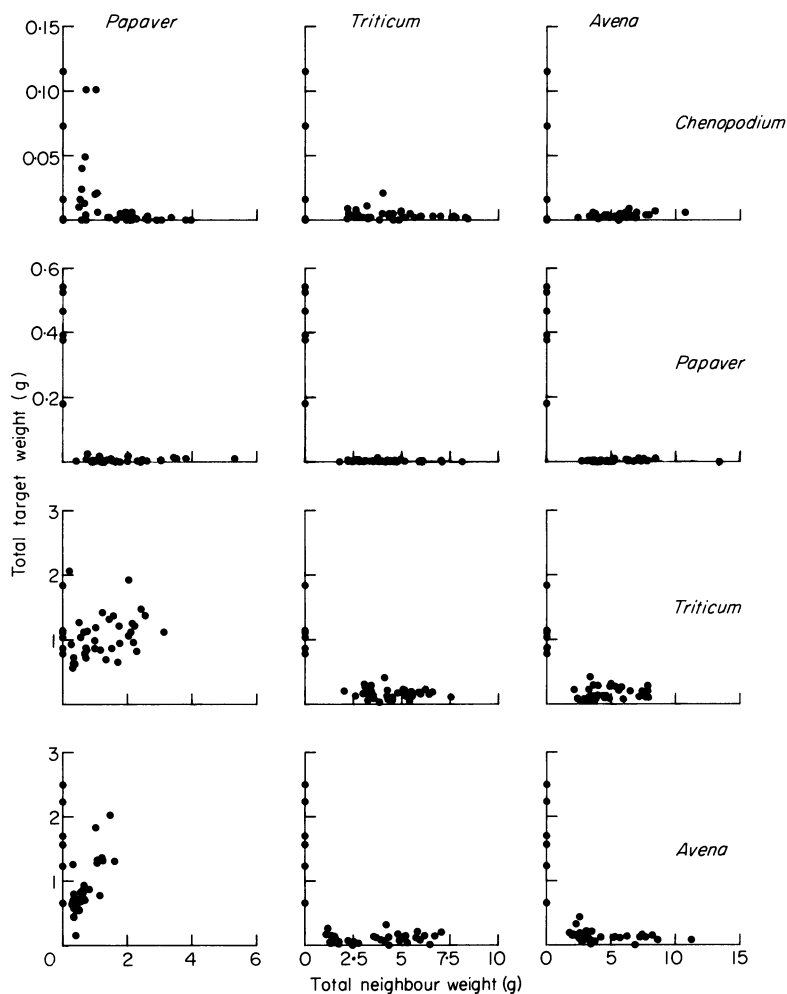


FIG. 2. Relationship between total target weight and total neighbour weight for twelve combinations of target and neighbour species. Names of the three neighbour species are listed across the top and of the four target species along the right side.

TABLE 2. R^2 for hyperbolic regressions of total target weight on initial neighbour density (a) and total neighbour weight (b). All relationships indicate competitive interactions. Sample size equals 42 except where noted.

Target species	Neighbour species		
	<i>Papaver</i>	<i>Triticum</i>	<i>Avena</i>
(a) Neighbour density			
<i>Chenopodium</i>	0.149	0.287	0.285
<i>Papaver</i>	0.905 ($n=41$)	0.908	0.907
<i>Triticum</i>	0.066	0.845	0.849
<i>Avena</i>	0.327	0.827 ($n=41$)	0.836
(b) Total neighbour weight			
<i>Chenopodium</i>	0.164	0.275	0.285
<i>Papaver</i>	0.905 ($n=41$)	0.907	0.907
<i>Triticum</i>	0.049	0.829	0.794
<i>Avena</i>	0.054	0.826 ($n=41$)	0.827

TABLE 3. R^2 for linear regressions of total target weight on initial neighbour density (a) and total neighbour weight (b) for pots with neighbour density > 0 . Sample size equals 36 except where noted. The directions of the correlations are shown in parentheses below each R^2 value. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Target species	Neighbour species		
	<i>Papaver</i>	<i>Triticum</i>	<i>Avena</i>
(a) Neighbour density			
<i>Chenopodium</i>	0.230** (-)	0.202** (-)	0.078 (-)
<i>Papaver</i>	0.004 ($n=35$) (-)	0.270*** (-)	0.032 (-)
<i>Triticum</i>	0.012 (+)	0.422*** (-)	0.397*** (-)
<i>Avena</i>	0.073 (-)	0.003 ($n=35$) (+)	0.240** (-)
(b) Total neighbour weight			
<i>Chenopodium</i>	0.194** (-)	0.053 (-)	0.109* (+)
<i>Papaver</i>	0.032 ($n=35$) (+)	0.032 (-)	0.044 (+)
<i>Triticum</i>	0.084 (+)	0.010 (-)	0.044 (+)
<i>Avena</i>	0.608*** (+)	0.040 ($n=35$) (+)	0.102* (-)

TABLE 4. Comparison of competitive effects among neighbour species and competitive responses among target species, averaged over all neighbour densities > 0 . Target weight is expressed as percentage of the mean value for isolated plants for each target species. Values are means \pm 95% confidence limits. Values with the same letters are not significantly different by a Mann-Whitney U -test ($P > 0.01$): a, b for within-row comparisons (among neighbours); w, x, y, z for within-column comparisons (among targets). Sample size equals 36 except where noted. *** $P < 0.001$.

	Neighbour species (Density > 0)			Kruskal-Wallis χ^2 (d.f. = 2)
	<i>Papaver</i>	<i>Triticum</i>	<i>Avena</i>	
<i>Chenopodium</i>	^w 35.8 \pm 24.3	^x 11.2 \pm 3.9	^y 10.3 \pm 2.0	0.50
<i>Papaver</i>	^x 1.3 \pm 0.5 ($n=35$)	^y 0.7 \pm 0.2	^x 0.8 \pm 0.2	3.75
<i>Triticum</i>	^y 93.6 \pm 10.1 ^a	^z 14.7 \pm 2.4 ^b	^y 14.2 \pm 2.8 ^b	71.4***
<i>Avena</i>	^z 51.2 \pm 7.9 ^a	^x 6.4 \pm 1.5 ^b ($n=35$)	^z 8.5 \pm 1.6 ^b	71.0***
Kruskal-Wallis χ^2 (d.f. = 3)	92.39***	78.70***	79.13***	

the pots with different neighbour densities. Therefore, we used the weight of target plants averaged over all densities of neighbours greater than zero as a simple index of the magnitude of the competitive interaction in each species combination (Table 4). The main advantage of this index over the coefficient of regressions of target performance over the entire density range is that it avoids the problem of the absence of very low values of neighbour density and, especially, neighbour weight (Figs 1 and 2). Because the drop in target performance is steepest at low neighbour density and weight, it is especially critical to have enough data points in this range to characterize their relationship accurately, if a regression approach is to be used.

Because size of isolated plants (neighbour density = 0) differs among target species

TABLE 5. Comparison of competitive effects among neighbour species and competitive responses among target species, including only target plants where total neighbour weight (NW) was between 3 and 4 g or 1 and 2 g. Target weight is expressed as percentage of the mean value for isolated plants of each target species. Values are means \pm 95% confidence limits, with sample size below each value. Values with the same letters are not significantly different by a Mann-Whitney *U*-test ($P > 0.01$); *a, b* for within-row comparisons (among neighbours); *x, y* for within-column comparisons (among targets). * $P < 0.5$, *** $P < 0.001$.

Target species	Neighbour species			Kruskal-Wallis χ^2 (d.f. = 2)	d.f.	1 < NW < 2g <i>Papaver</i>
	<i>Papaver</i>	3 < NW < 4g <i>Triticum</i>	<i>Avena</i>			
<i>Chenopodium</i>	^x 1.7 \pm 5.4 ^a 4	^{xy} 10.1 \pm 9.4 ^a 7	^y 9.5 \pm 4.9 ^a 7	6.05*	2	^y 39.2 \pm 58.1 11
<i>Papaver</i>	^x 2.3 \pm 1.6 ^a 4	^x 0.8 \pm 0.5 ^a 10	^x 0.6 \pm 0.3 ^a 10	7.17*	2	^x 0.9 \pm 0.6 17
<i>Triticum</i>	99.0 \pm 0 1	^y 15.5 \pm 7.1 ^a 9	^y 14.4 \pm 6.0 ^a 13	—	—	^z 93.3 \pm 18.1 10
<i>Avena</i>	— 0	^y 6.9 \pm 4.0 ^a 3	^y 8.1 \pm 3.7 ^a 3	—	—	^z 85.3 \pm 19.2 3
Kruskal-Wallis χ^2 (d.f. = 3)	—	17.43***	21.81***			32.28**

(Table 1) the data for target weight in Table 4 are expressed as a percentage of the mean weight of isolated plants to facilitate comparisons of response among target species. A potential problem with this index is that inaccuracy in the estimate of mean size of isolated plants could bias the comparisons of competitive response in some way. (Use of percentage reduction rather than actual target weight has no impact on the statistical comparisons of competitive effects among neighbour species on a given target species because all values are divided by the same constant.) This problem is most likely to affect the comparisons involving *Chenopodium* because its growth in isolation was much more variable than the other target species (Table 1).

The rankings of effects of the three neighbour species are consistent over all four target species: the two grass neighbour species always cause similar, non-significantly different reductions in target plant weight and these effects are much greater (significantly so in two of the four target species) than the reductions in growth due to *Papaver* neighbours (Table 4). This is despite the fact that the range of *Papaver* neighbour densities was twice that of the grass neighbours.

The rankings of the response of the four target species are also generally consistent among neighbour species: *Papaver* target plants have a significantly greater percentage reduction in growth than all three other target species in the presence of all three neighbour species and *Triticum* target plants have the least reduction in growth in the presence of all three neighbour species (significantly so in two of three neighbour species; Table 4). *Avena* and *Chenopodium* have intermediate responses to neighbours that are statistically equivalent in two of three neighbour species.

These comparisons of competitive effects and responses over a range of densities are confounded by differences among neighbour species in size and total weight of neighbours. The smaller competitive effect of *Papaver* may be a consequence of its much lower total biomass at a given density (Fig. 2). If the hierarchy of effects is related to size of plants, then adjusting for weight of neighbours should eliminate the difference in effect between the grasses and *Papaver*. To adjust for neighbour weight, we compared mean

TABLE 6. Total neighbour weight for all densities greater than 0 for each species combination. Significant overall target effects (down columns) indicate that the target species has a significant effect on total neighbour weight. Values are means \pm 95% confidence limits; values in a column with the same letter are not significantly different ($P > 0.01$). ** $P < 0.01$, *** $P < 0.001$.

Target species	Neighbour species		
	<i>Papaver</i>	<i>Triticum</i>	<i>Avena</i>
<i>Chenopodium</i>	1.72 \pm 0.33 ^a	4.62 \pm 0.63 ^a	5.65 \pm 0.85 ^a
<i>Papaver</i>	1.74 \pm 0.36 ^a	4.09 \pm 0.50 ^{ab}	5.23 \pm 0.71 ^{ab}
<i>Triticum</i>	1.30 \pm 0.27 ^a	4.58 \pm 0.77 ^a	4.59 \pm 0.58 ^{bc}
<i>Avena</i>	0.62 \pm 0.12 ^b	3.67 \pm 0.65 ^b	4.31 \pm 0.80 ^c
Kruskal-Wallis χ^2 (d.f. = 3)	43.42***	6.36 ^{ns}	15.11**

TABLE 7. Root:shoot ratio for isolated plants ($n=6$) and plants grown with density > 0 of neighbours ($n=36$ except as noted). Dead target plants were not included. Values are means \pm 95% confidence limits. Values in a row with the same letter are not significantly different by a Mann-Whitney U -test ($P > 0.01$).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Target species	Isolated (density = 0)	Neighbour species (density > 0)			Kruskal-Wallis χ^2 (d.f. = 3)
		<i>Papaver</i>	<i>Triticum</i>	<i>Avena</i>	
<i>Chenopodium</i>	0.119 \pm 0.044 ^a $n=4$	0.367 \pm 0.094 ^b $n=35$	0.296 \pm 0.55 ^b $n=32$	0.302 \pm 0.067 ^b $n=35$	10.44*
<i>Papaver</i>	0.736 \pm 0.543 ^a	0.356 \pm 0.172 ^a $n=28$	0.207 \pm 0.049 ^a $n=33$	0.235 \pm 0.046 ^a $n=33$	6.94 ^{ns}
<i>Triticum</i>	1.567 \pm 0.615 ^a	3.922 \pm 0.542 ^b	0.572 \pm 0.56 ^c	0.894 \pm 0.128 ^d	73.99***
<i>Avena</i>	1.085 \pm 0.212 ^a	3.607 \pm 0.686 ^b	0.398 \pm 0.151 ^c $n=33$	0.331 \pm 0.55 ^c $n=35$	76.45***

percentage of isolated target weight across neighbours or targets for a restricted range (1 g) of neighbour weight values.

For all target-neighbour combinations except *Papaver* neighbours on both grasses as targets, at least three pots had a neighbour weight between 3 and 4 g (Table 5). The magnitude of differences in effect between species are similar to the values averaged over all densities greater than zero (Table 4). However, there are no significant pairwise differences in effect within or between growth forms for this range of neighbour weights, probably because of the smaller sample sizes. The trends are consistent with those from data averaged over all densities except that for *Chenopodium* as target, *Papaver* has a (non-significantly) stronger per-unit biomass effect than the two grasses (Table 5).

Comparisons of response adjusted for neighbour weight can only be made for response to the two grass neighbours and are consistent with the data averaged over all neighbour weights (Table 4). In both cases, *Papaver* tends to be a significantly poorer competitor in terms of response and *Triticum* the best, while the two grasses and *Chenopodium* always have statistically equivalent responses. Because response could not be compared among all targets to *Papaver* neighbours for neighbour weights between 3 and 4 g, the last column in Table 5 shows percentage of isolated target weight for neighbour weights between 1 and 2 g for *Papaver* as neighbour only (even at the lowest density, grass neighbours almost always weighed more than 2 g; see Fig. 2). Again *Papaver* is the weakest competitor in terms of response and *Triticum* the strongest. In addition, *Chenopodium* shows up as a distinctly weaker response-competitor than both grasses. Thus, despite the small sample

sizes, there are still some significant differences in response among target species for the 3–4 g or 1–2 g range of neighbour weights (Table 5).

The occurrence of fewer pots with *Papaver* neighbour biomass between 3 and 4 g for the two grasses as targets than for *Papaver* or *Chenopodium* as targets (Table 5) suggests that the targets may be having some influence on the neighbours. Table 6 contains mean total neighbour weight for each species combination, averaged over all densities > 0. The hierarchies of effect of targets on neighbours are largely consistent with the hierarchy of effect of neighbours on targets in that the grass targets have greater effects on weight of all neighbour species than do the dicotyledon targets. However, *Avena* appears as a distinctly stronger competitor than *Triticum*. In addition, these data give a rough idea of the position of *Chenopodium* in the effect hierarchy. For all three neighbour species, *Chenopodium* is more similar to *Papaver* in effect than it is to *Avena*, to which it was most similar in response (Tables 4 and 5).

The analyses thus far have considered the effects of neighbours on total target weight (root + shoot). There were also effects of neighbours on allocation of the targets to roots v. shoots. The four target species have very different root:shoot ratios when grown with no neighbours: *Chenopodium* has a very small root:shoot ratio, *Papaver* is intermediate, and the two grasses have the highest root allocation (Table 7). For all target species but *Papaver* the presence of neighbours of any species results in a significant change in root:shoot ratio (Table 7). However, the direction of change in root:shoot ratio is fairly specific to each species combination. The presence of *Papaver* neighbours is associated with an increase in root allocation by *Chenopodium* and grass targets, but with a decrease by *Papaver* targets. The presence of both grasses as neighbours results in an increase in *Chenopodium* root:shoot ratios but a decrease in root:shoot ratio for the other three target species (non-significant for *Papaver*). Both grasses as targets respond to grass neighbours by significantly decreasing root allocation, but to *Papaver* neighbours by significantly increasing root allocation.

DISCUSSION

As is typical in studies of both intraspecific and interspecific competition in plants, the effect of increasing density of competitors is strongly non-linear, with a large decrease in plant size due to any neighbours at all and smaller effects of adding still more neighbours (Harper 1977; Watkinson 1981; Weiner 1982, 1984; Spitters 1983; Silander & Pacala 1985; Pearlt & Foin 1985; Miller & Werner 1987; Goldberg 1987). Up to 91% of the variance in target weight can be explained by a simple non-linear function of density or biomass of neighbours. Most previous neighbourhood experiments have been concerned only with intraspecific competition and researchers have reported R^2 values ranging from 1% to 86% in natural and experimental monocultures (Fowler 1984; Liddle, Budd & Hutchings 1982; Mithen, Harper & Weiner 1984; Silander & Pacala 1985; Waller 1981; Weiner 1982, 1984). Values for intraspecific competition in this study range from 83 to 91% and for interspecific competition from 5% to 91%. Abundance of conspecific neighbours does not consistently explain more variance in target growth than abundance of heterospecifics.

The occurrence of extremely high R^2 values in this study may have resulted from the 7–9 day time lag in planting targets, leading to a strong initial size advantage to neighbours and so to very strong effects on the targets. A number of studies have shown a large competitive advantage from earlier germination (Black & Wilkinson 1963; Ross & Harper 1972; Watkinson, Lonsdale & Firbank 1983; Dolan & Sharitz 1984). An

additional reason may be that the R^2 values in Table 2 include target plants with no neighbours. Almost all of the other published neighbourhood experiments were conducted by mapping plants in large field plots or greenhouse flats and so probably includes few or no plants without any competitors. When the isolated plants are excluded, the target–neighbour relationships in the current study became linear in almost all cases, and the proportion of variance in target weight explained by neighbour density or weight decreases to 40–55% (intraspecific) and 0–56% (interspecific).

Hierarchies of competitive effect and competitive response

In this study, we found that the ranking of competitive effect among neighbour species was independent of the target species considered, and that the ranking of competitive response among target species was independent of the neighbour species considered. A number of previous studies have also shown that competitive ability of a plant species is often independent of the species with which it is competing (e.g. Welbank 1963; Obeid 1965; Trenbath 1974; Trenbath & Harper 1973; Mahmoud & Grime 1976; Miller & Werner 1987; but see Haizel & Harper 1973). The important question then is what traits of each species determine its relative competitive effect and response? For competitive effect, one possibility is simply plant size—larger plants are likely to have a greater competitive effect because they can take up more resources (Connolly 1986). Several studies have shown that the ranking of competitive effect is correlated with the ranking of average plant size or total abundance of the neighbour or competitor species (e.g. Obeid 1965; Peart & Foin 1985; Miller & Werner 1987; Goldberg 1987). Similar results were obtained in this experiment: the two grasses grow much larger at a given density than does *Papaver* and they had larger competitive effects. However, if the magnitude of competitive effect exerted by a species is solely a matter of plant size, adjusting for plant size should eliminate the hierarchy. For example, three field experiments on interspecific competition found that significant differences among species in competitive effect disappeared when plant size was taken into account (Peart & Foin 1985; Miller & Werner 1987; Goldberg 1987). However, this does not seem to be the case for the species used in these experiments because the hierarchy of competitive effects exists even when the comparisons are limited to a restricted range of neighbour weights. Plants of almost all the target species growing with 3–4 g of grass neighbours were much smaller than target plants growing with the same weight range of *Papaver* neighbours.

There are two limitations to this test of whether differences in competitive effect are solely due to differences in plant size. First, weight is only one measure of size. If, for example, competition is mostly for light, leaf surface area or plant height or both might be a better measure of plant size for considering the resources made unavailable to the targets by the neighbour plants. This could explain the greater effect of the grasses because they probably have a greater leaf surface area per unit of total plant weight. On the other hand, the vertical orientation of grass leaves should tend to reduce the amount of shade cast per unit surface area. Secondly, and of more general importance, the magnitude of competitive effect experienced by a target plant integrates competitive effects experienced over the entire experiment. If the neighbour species had different phenologies of growth, final neighbour weight may be a poor indicator of the relative size of neighbours of different species earlier in the experiment. Although we have no data on neighbour weights before the final harvest, the much larger seed weight of the grasses suggests that their initial growth rates (g day^{-1}) were probably much greater than for the *Papaver* neighbours (Black 1957; Cideciyan & Malloch 1982). Furthermore, many of the grass

neighbours were flowering or setting seed by the end of the experiment and probably had reduced vegetative growth at this time. Therefore, it is possible that the greater effect of grass neighbours than *Papaver* neighbours of similar final weights is because they have a larger initial size advantage.

Similar arguments about the consequences of plant size can be made for competitive response: plants that are large relative to their competitors should be less affected by the presence of competitors. The ranking of competitive responses among the target species is partially consistent with this argument—growth of the two grasses is reduced much less by the presence of competitors than is growth of *Papaver*. However, *Chenopodium* targets are much better response competitors than expected from their size and from their seed weight. *Chenopodium* and *Avena* have very similar responses to competition but *Chenopodium* seeds are only 2% of the weight of *Avena* seeds and the size of *Chenopodium* plants without neighbours is only 2% of the size of *Avena* plants without neighbours.

This unexpected strong response-competitive ability of *Chenopodium* may be a statistical artefact. Because the confidence interval around the estimate of mean plant size in isolation was so much larger for *Chenopodium* than for the other target species, the calculation of percentage reduction in growth from that with no competition for this species may be less accurate. If the true mean growth in isolation is actually much higher, then the true percentage reduction in growth due to neighbours would also be much greater. However, when percentage reduction was recalculated using the upper limit of the 95% confidence interval around the mean growth in isolation, rather than the mean itself, *Chenopodium* remains an unexpectedly strong response-competitor. From the data available it is not clear why *Chenopodium* is such a strong response-competitor.

Competitive effect vs. response

Expectations of how effect and response hierarchies should be related to each other depend on the traits that determine the ranking for each aspect of competitive ability. If both are related to absolute growth rate or size as indices of total use of resources, then they obviously should be positively related. This appeared to be the case here for all species but *Chenopodium*: *Papaver* is the weakest competitor in terms of both effect and response, and the grasses are the strongest competitors in terms of both effect and response. However, where plants are already at a size disadvantage (as with later-germinating seedlings or seedlings germinating in already established vegetation), competitive response may be independent of size or growth rate and operate through tolerance of low resource availability rather than ability to acquire a large share of the limited resources. Thus, competitive effect and response might be uncorrelated or even negatively correlated as Grime (1977) and others have argued. Unfortunately, it is still difficult to fit the unexpectedly strong competitive response of *Chenopodium* into this scheme; as a weedy annual it is probably not particularly shade-tolerant at least, although we have no data directly comparing its tolerance of low resource levels with the other species used in these experiments.

These arguments about the relationship between plant size or growth rate and competitive effect vs. response lead to one further prediction. If competitive effects are more likely to be closely related to plant size than are competitive responses, comparisons of competitive ability on a per-gram basis should lead to equivalence of competitive effects but not of competitive response (Goldberg & Werner 1983). Miller & Werner (1987), and Peart & Foin (1985) report results from field experiments that are consistent with this prediction: significant differences in response among several 'target' species, but

no significant differences in effect of the same species as 'neighbours' when neighbour abundance is taken into account. Our results are also partially consistent with this prediction. We found equivalent effects between the two grass species (with or without adjusting for neighbour size) but significant differences in response.

Biomass allocation

In most published competition experiments, results are reported for competitive effects only on above-ground biomass or growth rates because of the difficulty of obtaining accurate estimates of root biomass, especially in the field. In those few studies that have reported effects of competition on below-ground biomass, increases (Snell & Burch 1975; Goldberg 1987), decreases (Bleasdale 1966; Goldberg 1987), and no change (Goldberg 1987; Werner 1987) in root allocation have all been found. Bleasdale (1966) suggested that the direction of change in allocation to roots may indicate the resource for which the species are competing; that is, increases in allocation to roots should reflect increased competition for water or nutrients while increases in allocation to shoots should reflect increased competition for light. This suggestion is supported by the generally consistent effects on root:shoot ratios of direct manipulations of resource availability in the absence of competitors (Bradshaw *et al.* 1964; Loach 1970; Snell & Burch 1975; Jaksic & Montenegro 1979; Werner 1987).

In this study, there were differences in the direction of change in the root:shoot ratio among the species combination. However, because the direction of change was not consistent within target or neighbour species, there is no indication that some species are consistently better competitors than others for a particular resource type. For example, *Papaver* neighbours sometimes were associated with a decrease in root:shoot ratio (*Papaver* targets) and sometimes with an increase (*Chenopodium* and grass targets). These inconsistencies are especially interesting given the strongly consistent hierarchies of competitive effect on and response of total target weight (root + shoot), and suggests that the relative importance of below vs. above-ground competition may vary in a much more species-specific manner than does response or effect in terms of reduction in total plant weight. More detailed interpretation of these results awaits information on how plants affect availability to above vs. below-ground resources and on how the same species respond to changes in availability of each resource.

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