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COMPETITION AMONG OLD-FIELD PERENNIALS AT DIFFERENT LEVELS OF SOIL FERTILITY AND AVAILABLE SPACE

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SUMMARY

(1) Competitive effects and responses to neighbours were examined by growing plants of three species (*Achillea millefolium*, *Dactylis glomerata* and *Vicia cracca*) singly and in intra- and interspecific pairs at low and at moderate substrate fertility. The effects of neighbours were distinguished from the effects of a reduction in available space by growing plants across a range of pot sizes.

(2) Focal plants were affected by a simple reduction in available space differently than by the presence of competing neighbours. The effects of neighbours were complex, and depended on the species that were competing and on how the effect was measured.

(3) Competition did not generally have greater negative effects on plant performance (using several measures of performance) at higher fertility levels and when more space was available. Nor was there a tendency for greater competitive effects at lower soil fertility and when space was more restricted. There were no apparent trade-offs in competitive abilities at different resource levels.

(4) The negative effects of competition on an individual plant's growth, for the poorer competitor of a pair, was greater if the neighbour was of a different species than if the neighbour was a conspecific.

(5) There was a generally consistent hierarchy of competitive effects and responses among species that reflected the hierarchy of initial seed sizes.

(6) Root:shoot ratios differed among species and were altered by available space (pot size), fertility level and neighbour identity. Root:shoot ratios were most variable in response to neighbour identity in *Achillea*, the poorest competitor, and least responsive in *Vicia*, generally the best competitor.

INTRODUCTION

The responses of individual plants to competitors, and the effects of individuals on their neighbours, have gained increasing attention as the limitations of studying the average effects of competition in mixed and monoculture stands have become more apparent (e.g. Mack & Harper 1977; Mithen, Harper & Weiner 1984). 'Neighborhood studies' have shown that the interactions between immediately adjacent plants may largely determine plant performance (e.g. Trenbath 1974; Mack & Harper 1977; Weiner 1982; Silander & Pacala 1985; Miller & Werner 1987; Goldberg 1987; Goldberg & Fleetwood 1987). The simplest possible competitive interaction is that between a pair of individuals. An examination of competitive effects and responses among such pairs may offer insight into the mechanisms by which plants of different species are able to acquire resources in the presence of competitors, and consequently dominate or fail to perform well in mixtures.

When plants compete in mixed stands, the density of the stand determines the average amount of space, nutrients, water and light available to individuals. Although all individuals will generally be smaller in denser stands as average access to resources

declines, at every density some individuals are able to grow much larger than others because they are able to acquire a disproportionate share of resources, presumably at the expense of others. In most experiments, the effects of competitors at increasing density are confounded with the simple effects of a reduction in the average amount of space, nutrients, etc., available per plant. However, one would expect that the restriction in root space available to a plant due to the presence of a stone in the soil, for example, would be fundamentally different from the restriction due to the presence of a competing neighbour. It is not possible to disentangle such effects by growing plants at a range of densities.

In order to distinguish the effects of differences in the average amount of space and nutrients available to a plant from the effects of a reduction in space and nutrients due to competition, we set up an experiment in containers of four sizes, at low and at moderate substrate fertility. The responses to inter- and intraspecific competitors were compared with plant performance without neighbours. Competitive effects of and responses to neighbours cannot be fully understood without knowing the potential for growth in the absence of competitors.

Three co-occurring old-field herbaceous perennials were used in the experiment: *Achillea millefolium* L., *Dactylis glomerata* L. and *Vicia cracca* L. (referred to subsequently by generic names). The competitive effects of *Dactylis* and the responses of the three species to different levels of competition and soil fertility in the field are discussed by Gurevitch & Unnasch (1989). *Achillea* is a small, rhizomatous, rosette-forming species with a limited, shallow root system, and is shaded by taller neighbours; *Vicia* is a weak-stemmed, nitrogen-fixing, low-growing vine; and *Dactylis* is a mid-sized, dominant, non-rhizomatous grass with an extensive fibrous root system. In the twenty-five-year-old field from which the seeds of these species were collected, *Dactylis* was dominant, *Vicia* was subdominant, and *Achillea* was a common, but never dominant, understorey component.

The experiment addressed the following general questions: (i) does a simple physical restriction in space have the same effect as the restriction due to the presence of a competing neighbour? (ii) Are the effects of competition among species pairs more severe when space or nutrients are highly restricted than when space or nutrients are present in greater amounts? (iii) Is the restriction in an individual plant's growth due to competition with a neighbour greater if the neighbour is the same species (presumably due to greater overlap of resource use) than if the neighbour is a different species (presumably due to greater disparities between individuals of different species)? Or (iv) does the species that produces the largest plants when individuals are grown alone always have the greatest negative effect on neighbours, and the species with smallest plants the least effect, or are competitive effects and responses more individualistic? Conventional analyses were combined with novel approaches to address these questions. The different analyses provide complementary information on how each species responded to competitors, restricted space and limited nutrients.

METHODS

Propagules (referred to henceforth as 'seeds') of *Achillea*, *Dactylis* and *Vicia* were collected during July and August 1988 from an old field at Brookhaven National Laboratory (41°N, 73°W) on eastern Long Island, New York. Seeds were scarified (*Vicia*) or stratified (other species) for up to twelve days and germinated on moist paper in Petri dishes in a growth chamber at 27 °C. *Vicia* seeds were treated with a commercial

Rhizobium inoculant. Seeds were put into Petri dishes on a staggered schedule so that all species would germinate at approximately the same time.

Seedlings were set into pots on 29 October 1988. The experimental design consisted of three crossed factors: (i) fertilization level, (ii) pot volume, and (iii) presence and identity of neighbour. Treatments are described in detail below. Each treatment combination was replicated five times (i.e. in five pots).

Plants were grown in Turface growth medium with nothing added (fertilization level = 0) or with 15–15–15 (N–P–K) Osmocote slow-release pelletized fertilizer (fertilization level = 1) at 1.5 g l^{-1} (a relatively low level of fertilization). All plants received supplemental fertilization on 15 November and 6 December as Peter's 20–20–20 (N–P–K) general-purpose liquid fertilizer at quarter strength and were watered with a dilute micronutrient supplement on 5 December.

Four sizes of square plastic pot were used: pot size 1 (5.7 cm wide, 0.08 l volume), pot size 2 (7.6 cm, 0.17 l), pot size 3 (8.9 cm, 0.25 l), and pot size 4 (10.2 cm, 0.45 l). Pot sizes were chosen so that shape remained approximately constant as volume increased. Of necessity, this approach confounds increased volume with increased surface area (but see Results). Pots were placed in a randomized grid on benches in a glasshouse at Stony Brook. Pots were re-randomized on 2 December to minimize position effects.

Plants of each species were grown singly (one plant pot^{-1}), and in pairs (two plants pot^{-1}) in all possible species combinations (intraspecific and interspecific) in all pot sizes and at both fertility levels. The response of each species as a 'focal plant species' to each 'neighbour species' was examined. The experiment consisted of nine species combinations, with a total of *c.* 600 plants in 360 pots.

Seven seedlings that died during the initial two weeks of the experiment were replaced with individuals of the same age and approximately the same size. Four seedlings subsequently died, and those pots were omitted from the final analyses. The eleven individuals that died were scattered among treatments and species, and the losses could not therefore be attributed to treatment-related mortality. Pots were watered thoroughly once daily until 2 December, and twice daily from 2 December until harvest so that differential drying would not be confounded with pot size. Plants were harvested on 28 January 1989, thirteen weeks after they were planted. Roots were washed free of Turface and separated by hand. Roots and shoots were dried at 50°C and weighed separately on an analytical balance. For conspecific species pairs, only data for one plant in each pot (the plant on the left when viewing the pot label) were used, except where total biomass pot^{-1} was calculated.

RESULTS

Competitive effects and responses were assessed using six different analyses: (i) analysis of variance of total dry mass individual^{-1} and of root:shoot ratios, calculated for all species together and for each focal species separately, in response to fertilizer level, pot size and neighbour identity (ANOVA analysis); (ii) a measure that contrasts the effects of competition with the effects of restricted space (VOLUME analysis); (iii) de Wit diagrams, which contrast interspecific and intraspecific effects (DEWIT analysis); (iv) total yield pot^{-1} in pots with single plants, intraspecific pairs, and interspecific pairs (TOTAL analysis); (v) an index of size disparity that compares interspecific with intraspecific effects across species, scaled for the sizes of plants grown alone (DISPA-

RITY analysis); and (vi) an index of competitive effects and responses, standardized to the size of plants grown alone (EFFECTS analysis).

Analyses of yield individual⁻¹ (ANOVA analysis)

Overall effects

There were large differences among species and among treatments in final dry mass individual⁻¹ (Fig. 1). The overall hierarchy of focal plant species biomass from smallest to largest was: *Achillea*, *Dactylis* and *Vicia*. This was probably a reflection of the hierarchy of mean seed sizes, with means (and variances) of 'seed' mass (g) for *Achillea*, *Dactylis* and *Vicia*, of 0.1468 (0.0017), 0.9401 (0.0450) and 24.3580 (39.7180), respectively, based on $n = 30$ 'seeds' for each species. In the field, mature *Dactylis* is generally largest, *Achillea* is smallest and *Vicia* is intermediate in biomass. In general, competition, lower fertility and smaller pot sizes reduced final plant mass. Roots completely filled most pots (except for *Achillea* in the largest pots) indicating that competition for root space was intense. *Vicia* roots were well-nodulated. In most pots, surface area was not completely occupied, suggesting that plants were competing primarily for limited root space.

An analysis of variance (ANOVA) was conducted of total dry mass (yield) individual⁻¹ to determine the significance of the main effects of focal plant species, neighbour species, pot size, fertilizer level and all interactions between these factors for all pots with two plants. All of the main effects were large and highly significant ($P < 0.0001$). In addition, all two-way interactions with focal plant species were highly significant ($P < 0.005$): each focal species responded differently to neighbour identity, fertilizer level and pot size. The three-way interaction between focal plant, neighbour and fertilizer level was also highly significant ($P < 0.002$). No other interactions were significant.

Biomass and root:shoot ratios of each species

Because each focal plant species behaved differently, the responses of each focal species to pot size, fertilizer level and neighbour species were analysed individually. Both final dry mass (yield) individual⁻¹ and root:shoot ratios were examined. The response of each species to competitors as well as the effect each species had as a neighbour were evaluated.

Total harvested biomass of *Achillea* focal plants was affected by the identity of neighbours species, by pot size and by fertilizer level (Fig. 1a, b). There was a distinct hierarchy of competitive effects on *Achillea* by neighbours, with *Achillea* having the least effect as a neighbour (intraspecific competition) and *Vicia* having the greatest effect (each neighbour species differed significantly from the others at $P < 0.05$ by a Duncan-Waller K -ratio means test). There was a significant interaction between neighbour and fertilizer level (Fig. 2). This interaction was due to the reduced competitive effect of *Vicia* at high fertility.

Root:shoot ratio (Table 1) in *Achillea* was also sensitive to neighbour identity, pot size (both at $P < 0.0001$) and fertilizer level ($P = 0.006$). There were no significant interactions. Smaller pots and reduced fertility resulted in relatively greater investment in roots at the expense of shoots. *Dactylis* neighbours elicited higher root:shoot ratios than *Achillea* or *Vicia* neighbours.

Neighbour species, pot size and fertilizer level all had large and significant effects on *Dactylis* biomass (Fig. 1c, d). No interactions were significant. *Achillea* neighbours had the smallest effect and *Dactylis* neighbours the greatest effect in reducing the biomass of *Dactylis* focal plants (the three neighbour species differed significantly from one another by a Duncan-Waller means test at $P < 0.05$).

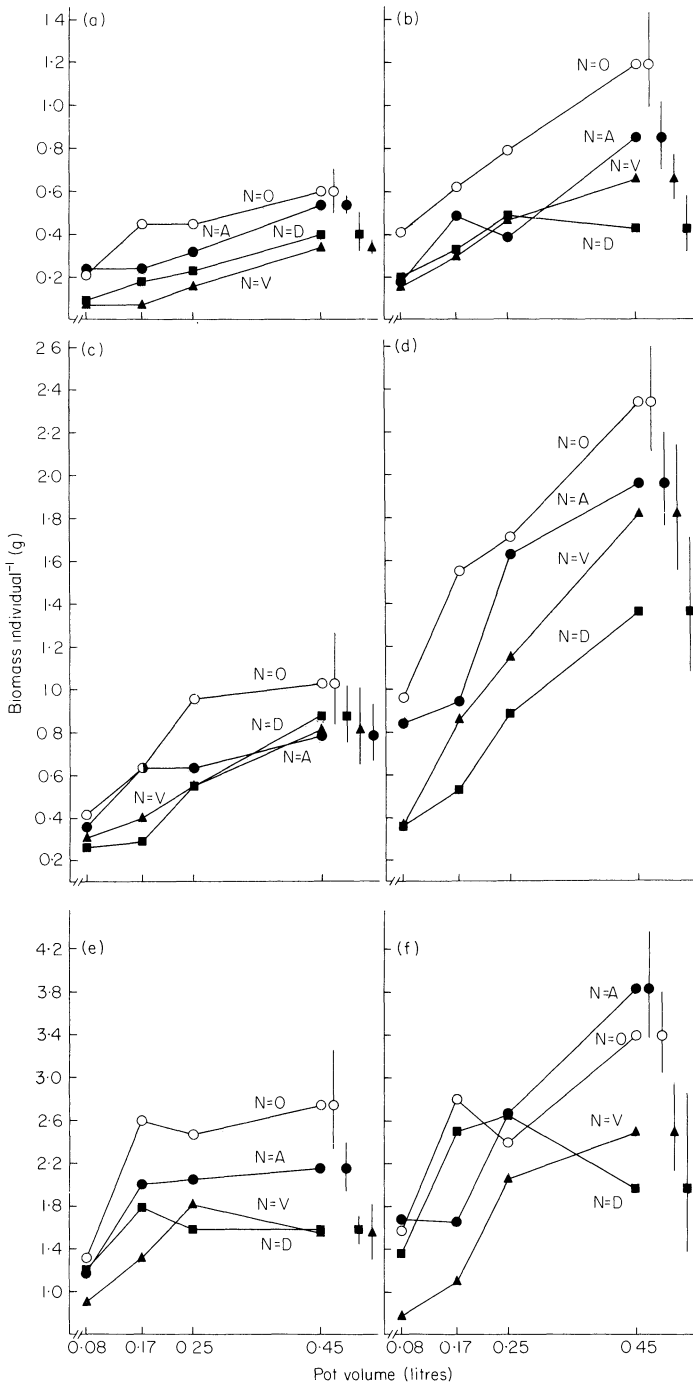


FIG. 1. Mean dry biomass individual⁻¹ (including shoots and roots) of *Achillea* (a), (b), *Dactylis* (c), (d) and *Vicia* (e), (f) focal plants grown with no neighbours (O, N=0), and in species pairs with *Achillea* neighbours (●, N=A), *Dactylis* neighbours (■, N=D), and *Vicia* neighbours (▲, N=V). Plants were grown at different pot volumes, with (a), (c), (e) no fertilizer added, or (b), (d), (f) fertilizer added. Standard errors of the means at the largest pot volumes are indicated to the right of the curves. Note that the scale for biomass in (e) and (f) differs from that in (a)–(d).

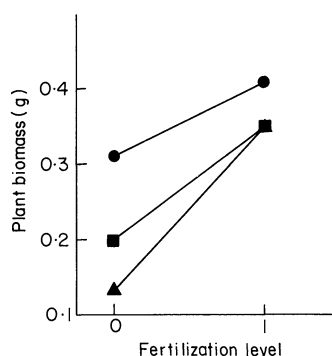


FIG. 2. Mean dry biomass individual⁻¹ for *Achillea* averaged across all pot sizes with no fertilizer added (0) and fertilizer added (1) and grown with *Achillea* (●), *Dactylis* (■) and *Vicia* (▲) neighbours.

Root:shoot ratio (Table 1) in *Dactylis* was responsive only to fertilizer level (at $P=0.0004$), with plants allocating proportionately less biomass to roots at the higher fertilizer level.

Total biomass of *Vicia* was affected by neighbour species and pot size, but not by fertilizer level (Fig. 1e, f). There was, however, a significant interaction between pot size and fertilizer level: fertilizer had little effect in small pots, and a substantial effect in larger ones. *Achillea* as a neighbour had the least effect on the growth of *Vicia* focal plants, and *Vicia* neighbours had the greatest effect (the differences among neighbours were significant at $P<0.05$).

TABLE 1. Mean root:shoot ratios (g dry root biomass:1.0 g dry shoot biomass) of *Achillea* (A), *Dactylis* (D) and *Vicia* (V) focal plants grown with *Achillea*, *Dactylis* and *Vicia* neighbours in the smallest and largest pots (pot size=1 and=4, respectively). Neighbour=0 indicates that the focal plant was grown with no neighbour. The standard error=1.10, and was approximately the same for all means; $n=5$ plants, except where noted by *, $n=4$. Means and standard errors were calculated on log-transformed values and back-transformed. Fertilizer level 0=no added fertilizer, 1=fertilizer added.

	Fertilizer level							
	0				1			
	Neighbour species				Neighbour species			
Focal species	0	A	D	V	0	A	D	V
Pot size=1								
A	1.32	2.23	2.58*	1.29	1.03	1.71	3.74	1.55
D	1.07	1.07*	1.29	1.24	1.01	0.93	1.01*	0.62
V	0.25	0.19	0.20	0.27	0.22	0.17	0.16	0.25
Pot size=4								
A	0.89	1.34*	2.13	1.09	0.91	1.00	1.60	0.75
D	0.89*	1.02	1.22	0.88	0.86	0.80	0.76	0.66
V	0.13*	0.13*	0.16	0.14	0.12	0.14*	0.18	0.11*

TABLE 2. Approximate volume in litres (interpolated from Fig. 1) at which biomass with a neighbour equals mean biomass of plants grown alone in the smallest (0.08 l) pots. Focal and neighbour species were *Achillea* (A), *Dactylis* (D) and *Vicia* (V). Fertilizer level 0 = no added fertilizer, 1 = fertilizer added.

Fertilizer level	Neighbour species					
	A		D		V	
	0	1	0	1	0	1
Focal species						
A	<0.08	0.15	0.22	0.21	0.31	0.22
D	<0.08	0.17	0.19	0.27	0.13	0.19
V	0.10	<0.08	0.10	0.09	0.17	0.21

Pot size had a large and significant effect on root:shoot ratio in *Vicia* ($P < 0.0001$, Table 1), with plants in smaller pots having reduced allocation to roots. The neighbour species \times pot size interaction also had a significant effect on root:shoot ratio ($P = 0.023$, Table 1). Root:shoot ratio of *Vicia* was considerably smaller than that of other species. Presumably, because of its climbing habit and nitrogen-fixing root nodules, root function (especially structural support and nutrient uptake) is accomplished with proportionately less root biomass.

Comparing the effects of neighbours with reduction in available space: plant size vs. pot volume (VOLUME analysis)

All species increased in size in response to greater available space in the absence of neighbours. This response was approximately linear with respect to volume, particularly over the three smallest pot sizes (Fig. 1a–f). By interpolation (from Fig. 1a–f), it is possible to estimate the volume of soil required to produce a plant grown in competition as large as one grown alone in the smallest pots (volume = 0.08 l). The larger the pot volume necessary, the more aggressive the neighbour. Two strictly equivalent individuals grown together should require exactly twice the space that one growing alone requires to reach the size of the plant grown alone. If a plant grown with a competitor requires more than double the volume of soil (i.e. more than 0.16 l) required by one grown alone to reach the same size, it can be inferred that the competitor is disproportionately preempting the space available for the focal plant. By estimating the pot volume required for plants grown in pairs to reach the biomass of plants grown alone, one can assess relative species' performance in the presence of competition and the relative aggression of neighbours. This approach offers an opportunity to distinguish competition for space from other effects.

Without fertilizer, *Achillea* plants grown without neighbours in the smallest pots were no larger than those with *Achillea* neighbours (Table 2); i.e. the presence of a conspecific neighbour apparently did not reduce the space available to *Achillea* focal plants. With fertilizer, the pot volume required was roughly doubled with *Achillea* neighbours. The volume needed with *Dactylis* neighbours was almost three times that for *Achillea* grown alone, and fertilizer did not alter the volume needed. With *Vicia* as a neighbour, *Achillea* plants grown without fertilizer needed larger pots than those with fertilizer to attain sizes comparable to those of *Achillea* plants grown alone.

In the presence of neighbours, *Dactylis* focal plants needed more space when fertilizer was added than in unfertilized pots to reach the size of plants grown alone (Table 2).

Dactylis neighbours usurped the greatest amount of space, and *Achillea* neighbours the least.

Achillea and *Dactylis* neighbours had essentially no effect on *Vicia* focal plants with or without fertilizer added at small pot sizes. Only *Vicia* as neighbours appropriated substantial amounts of available space; *Vicia* focal plants with *Vicia* neighbours required more than twice the pot volume to attain the same size as *Vicia* plants grown alone. The volume required was slightly greater with than without fertilizer.

Intra- vs. interspecific competition (DEWIT analysis)

Intra- and interspecific competitive effects were compared with a simplification of the conventional de Wit approach (mixed and monoculture pairs of plants were used rather than stands consisting of many plants) at each pot size and fertilizer level. This is analogous to examining a replacement series across a range of densities, with plants in the smallest pots at the highest density (per unit area of pot surface or per unit volume of growth medium available). Replacement series experiments have been criticized (e.g. Inouye & Schaffer 1981; Jolliffe, Minjas & Runeckles 1984; Connolly 1986), particularly when the interpretation of species' competitive abilities is based on an experiment conducted at a single density. While they may be inadequate as the sole measure of competitive interactions, de Wit diagrams remain a useful descriptive tool and can be very helpful when used in conjunction with other analyses. There is a large body of published glasshouse experiments on plant competition that have relied on de Wit diagrams and associated indices. In the present paper, they serve not only to clarify the comparison of inter- vs. intraspecific effects, but also to relate the results of this study to those of previous investigations.

Achillea was in general a poor competitor (Fig. 3), reaching moderate sizes in the presence of interspecific competition only in the largest pots and with the addition of fertilizer. In most cases *Vicia* and *Dactylis* had a greater effect on *Achillea* than *Achillea* had on itself, and *Achillea* had a smaller competitive effect on *Vicia* and *Dactylis* than these species had on themselves (e.g. the relative yields for *Achillea* when grown with *Vicia* were c. 0.25, while the relative yields for *Vicia* were c. 0.65 with *Achillea* as its neighbour). The effect of *Achillea* on its neighbours was substantially greater without fertilizer, especially in larger pots. Under these conditions the effect of *Achillea* on its neighbours approached that of the other species, despite the much smaller size of *Achillea* plants.

Dactylis was generally affected less by *Achillea* and *Vicia* than by competition from other *Dactylis* plants, particularly at the higher fertilizer level. Larger pot sizes and lower fertilizer level increased interspecific competitive effects on *Dactylis* until they were similar to intraspecific effects. *Dactylis* had a strong negative effect on *Achillea* (discussed above). The effect of *Dactylis* on *Vicia* became substantial only at larger pot sizes, and was greater without fertilizer. When large pot size was combined with low fertility, the competitive effect of *Dactylis* on *Vicia* was equal to or even greater than that of *Vicia* on itself (e.g. in Fig. 3c, d, at pot sizes 3 and 4 with fertility level = 0, the lines for *Vicia* become straight or even concave upward, indicative of relative yields < 0.5; see also Fig. 1e). The substantial competitive effects of *Dactylis* contrast with the considerably smaller size of *Dactylis* plants in comparison with *Vicia* plants.

Vicia plants were largest and in general were least affected by competitors. At larger pot sizes, *Achillea* and *Dactylis* neighbours approached the effects of intraspecific competition on *Vicia*, despite their smaller sizes.

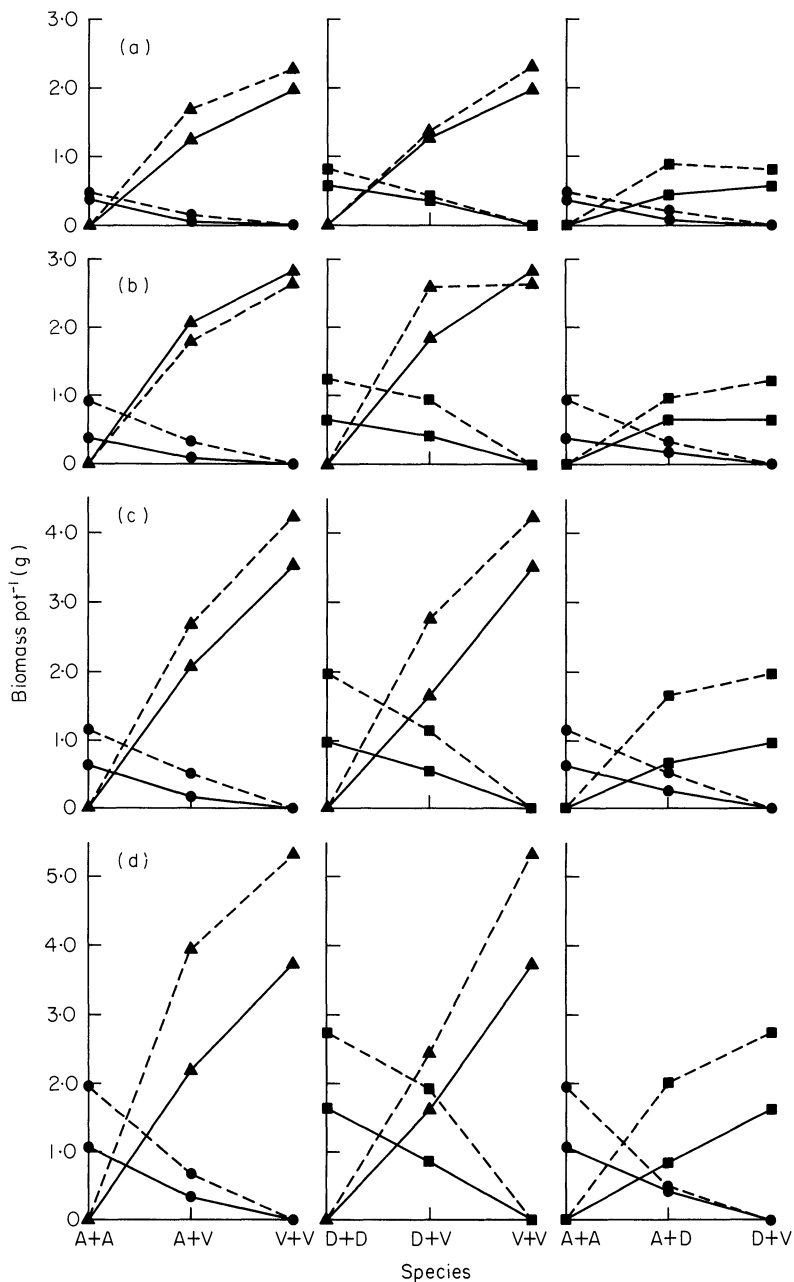


FIG. 3. Replacement diagrams at four pot sizes for plants grown with no fertilizer added (solid lines) and with fertilizer added (dashed lines). Soil volume pot⁻¹ was (a) 0.08 l, (b) 0.17 l, (c) 0.25 l and (d) 0.45 l. Species combinations were: *Achillea* and *Achillea* [A + A; biomass of *Achillea* pot⁻¹ (●)], *Achillea* and *Vicia* [A + V; biomass of *Vicia* pot⁻¹ (▲)], *Vicia* and *Vicia* (V + V), *Dactylis* and *Dactylis* [D + D; biomass of *Dactylis* pot⁻¹ (■)], *Dactylis* with *Vicia* (D + V), and *Achillea* with *Dactylis* (A + D). Yield includes dry biomass of shoots and roots.

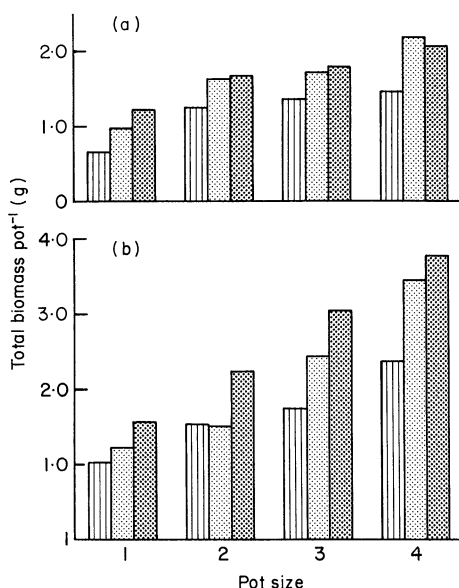


FIG. 4. Total dry biomass (g) pot⁻¹ (shoots plus roots of all plants grown in each pot), for pots with (a) no fertilizer added ($F=0$), and (b) with fertilizer added ($F=1$). Mean values for total pot biomass are plotted at each of the four pot sizes (0.08 l, 0.17 l, 0.25 l and 0.45 l), for pots with plants grown alone (left bar), for pots with intraspecific pairs (centre bar), and for pots with interspecific pairs (right bar).

Total yields pot⁻¹ (TOTAL analysis)

The total biomass produced pot⁻¹ varied with the experimental treatment (Fig. 4). Total biomass pot⁻¹ differed significantly among pots with plants grown alone (no competition), in intraspecific pairs, and in interspecific pairs ($F=14.69$, $P<0.0001$). The greatest total biomass was produced by interspecific pairs, an intermediate biomass by intraspecific pairs, and the least biomass was produced by plants grown alone ($P<0.05$; Duncan-Waller means test).

As might be expected, fertilizer level and pot size also affected total pot biomass, with significantly greater biomass produced at higher fertility ($F=33.90$, $P<0.0001$) and in larger pots ($F=27.24$, $P<0.0001$; each of the four pot sizes differed from the others; Duncan-Waller means test). As the fertilization-level-pot-size interaction was also significant ($F=4.36$, $P<0.005$), the effect of pot size was tested separately for the two fertilization levels (no other interactions were significant). With no added fertilizer, there was less distinction among pot sizes and also among competition levels. While both of these effects were statistically significant, only the smallest pot size differed from the other three sizes, which did not differ from one another (Duncan-Waller means test). And while pots with plants grown with no competition differed from those grown with a neighbour, intra- and interspecific pairs did not differ from one another. At the higher fertility level, each pot size differed from all others, and pots with plants grown alone, in intraspecific pairs, and in interspecific pairs all differed from one another in total biomass pot⁻¹ ($P<0.05$; Duncan-Waller means test).

Intra- vs. interspecific competition: size disparity among individuals (DISPARITY analysis)

The disparity in biomass between individuals in competition is one indication of the

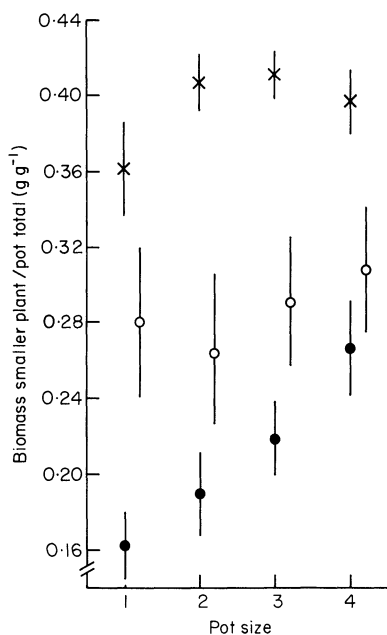


FIG. 5. Proportion of total pot biomass contributed by the smaller member of a pair of plants for intraspecific (x) and interspecific (●) pairs, and for plants grown alone (○) at four pot sizes (0.08 l, 0.17 l, 0.25 l and 0.45 l). Values did not differ significantly for the two fertility levels, which are averaged together. Values plotted are means (± 1 S.E., $n=6$).

intensity of competition between them. The size disparity among individuals was measured when plants were grown singly and when they were grown with neighbours to distinguish species-specific differences in size from differences caused by competition with neighbours. For plants grown with neighbours, the fraction of total pot biomass contributed by the smaller individual (regardless of species) in each pot was calculated, and the results for intraspecific pairs were compared with those for interspecific pairs at each pot size. The smaller individual of a pair fared substantially better on average with a neighbour of the same species than with one of a different species. This is reflected in the large, statistically significant differences between intra- and interspecific pairs in the proportion of biomass contributed by the smaller individual (Fig. 5; $F=177.72$, $P<0.0001$).

A comparable measure for plants grown alone was derived as follows. Using the mean biomass of individually grown plants at each pot size and fertility level, each of the three possible interspecies combinations was examined. For each species combination, the mean biomass of the smaller species was divided by the sum of the mean biomass of the two species (Fig. 5). This offered a way to compare species of different sizes when plants were grown without competitors and when they were grown in competing pairs. The size disparity among species was substantially less when plants were grown alone than when plants were grown in interspecific pairs. Consequently when plants were grown alone, the average contribution of the smaller plant to the total biomass of a 'pair' was considerably larger than when the same species were grown together in competing pairs (Fig. 5).

The smaller plant in a pot contributed proportionately less in small pots than in larger ones (the effect of pot size was statistically significant; $F=4.20$, $P<0.007$). An increase in

substrate fertility did not have any effect on the proportion of biomass contributed by the poorer competitor of a pair. No interactions between factors were significant.

When the effects of pot size were analysed separately for intra- and interspecific pairs, pot size had a significant effect for inter- but not for intraspecific pairs. For interspecific pairs the smaller plant in a pot was proportionately smaller when space was more restricted (pot size was significant, with $F=4.46$, $P=0.005$).

Index of competitive effects and responses (EFFECTS analysis)

Most analyses of competition, including replacement series, fail to disentangle fully competitive effects and responses from differences in potential growth (i.e. inherent size differences among species). This is because plants grown in interspecific competition are compared with those grown in intraspecific competition, while plants grown singly, without competitors, are rarely included in the experimental design or used as a basis for comparison [but see Parrish & Bazzaz (1982) and Goldberg & Fleetwood (1987)]. To examine competitive effects and responses scaled for absolute plant sizes, a standardized measure,

$$\frac{\alpha_{ij}}{\alpha_{i0}},$$

where α_{ij} = mean dry mass of species i when grown with a neighbour of species j , and α_{i0} = mean dry mass of species i when grown with no neighbour, was calculated for each pot size at each fertilizer level (Table 3). From this an index of the general competitive response to neighbours, R_i , was derived for each focal species i , where

$$R_i = \frac{\sum_{j=1}^n \frac{\alpha_{ij}}{\alpha_{i0}}}{n}$$

summed over all j neighbour species at each pot size and fertilizer level. Likewise, a corresponding index was derived of the competitive effect that each species j has when it is a neighbour, E_j , summed over all of the i species with which it is grown:

$$E_j = \frac{\sum_{i=1}^n \frac{\alpha_{ij}}{\alpha_{i0}}}{n}.$$

Finally, the overall competitive effect and response of each species was calculated as the grand means of R_i and E_j over all pot sizes and fertilizer levels. Values close to 1.00 indicate little or no competitive effect or response, values > 1.00 suggest mutualism or partial non-overlap of resource or space use, values of $c. 0.50$ indicate equivalent competitive abilities and equal sharing of resources, and values < 0.50 indicate unequal use of resources by the two competing species. Note that as the competitive effect of a species as a neighbour becomes more severe, the value of E_j for that species becomes smaller. As the response of a species to its neighbours becomes greater (i.e. it suffers more from competitors) the value of R_i for that focal species becomes smaller.

The three species differed from one another in competitive effects and responses (differences were statistically significant; at low fertility, Kruskal-Wallis $\chi^2=10.83$, $P<0.005$ for E_j , and $\chi^2=10.60$, $P<0.005$ for R_i ; at high fertility, Kruskal-Wallis $\chi^2=6.15$, $P<0.05$ for E_j , and $\chi^2=7.72$, $P<0.025$ for R_i). However, there were no clear trends across species for R_i s or E_j s over increasing pot size. Differences in the values for R_i

TABLE 3. Competitive effects (E_j) and responses (R_i) at each pot size. Index of competitive effects and responses are means across all species of the α_{ij}/α_{i0} for each focal plants species grown with each neighbour species. Values for α_{ij}/α_{i0} are the mean dry mass of focal species i when grown with a neighbour j , divided by the mean dry mass of species i when grown singly. Species were *Achillea* (A), *Dactylis* (D) and *Vicia* (V). Fertilizer level 0 = no added fertilizer, 1 = fertilizer added.

		Fertilizer level							
		0				1			
		Neighbour species, j							
Focal species, i :		A	D	V	R_i	A	D	V	R_i
Pot size = 1									
A		1.14	0.45	0.34	0.64	0.43	0.48	0.39	0.43
D		1.15	0.71	0.85	0.90	0.88	0.38	0.39	0.55
V		0.89	0.91	0.67	0.82	1.07	0.87	0.50	0.81
E_j		1.06	0.69	0.62		0.79	0.58	0.43	
Pot size = 2									
A		0.52	0.40	0.15	0.36	0.79	0.53	0.49	0.60
D		1.00	0.45	0.63	0.69	0.61	0.34	0.56	0.50
V		0.77	0.69	0.51	0.66	0.59	0.89	0.39	0.62
E_j		0.76	0.51	0.43		0.66	0.59	0.48	
Pot size = 3									
A		0.72	0.50	0.36	0.53	0.49	0.63	0.59	0.57
D		0.67	0.57	0.57	0.60	0.94	0.52	0.67	0.71
V		0.83	0.64	0.74	0.74	1.11	1.11	0.86	1.03
E_j		0.74	0.57	0.56		0.72	0.75	0.71	
Pot size = 4									
A		0.90	0.68	0.57	0.72	0.71	0.36	0.55	0.54
D		0.77	0.85	0.79	0.80	0.84	0.58	0.78	0.73
V		0.78	0.57	0.56	0.64	1.13	0.58	0.74	0.82
E_j		0.82	0.70	0.64		0.89	0.51	0.69	
Overall E_j		0.85	0.62	0.56		0.80	0.61	0.58	
Overall R_i		0.56	0.75	0.71		0.54	0.62	0.82	

and E_j between fertilized and unfertilized pots across species were likewise not statistically significant (Mann-Whitney U -test). *Achillea* had the smallest overall effects on others (largest E_j) and experienced the greatest reduction from competing neighbours (smallest R_i). Fertilization had little effect on either the competitive effect or response of *Achillea*. *Dactylis* and *Vicia* were generally well-matched in competitive effects and responses, except that competitors had a more severe effect on *Dactylis* at high fertility, while the addition of fertilizer improved the competitive response of *Vicia*.

DISCUSSION

Space vs. competitors

Focal plants were affected differently by a simple reduction in available space than by the presence of competing neighbours. The restrictive effects of neighbours were complex, and depended on the species that were competing and on how the effect was measured. For some species pairs, competition had a negative effect that was disproportionately greater than the effect of a simple reduction in space available.

Several lines of evidence support these conclusions. Data on yield (total dry mass) individual⁻¹ and on root:shoot ratios demonstrated that limitations due to neighbours were different than the effects of limited volume (Fig. 1; ANOVA analysis). For example, all plants were smaller and had greater root:shoot ratios in small pots than in large pots (without neighbours). That is, a simple physical restriction in space resulted in smaller plants with greater root:shoot ratios. However, the effects of neighbours on biomass and on root:shoot ratios were more intricate, and varied considerably among focal plants and neighbour species (Fig. 1, Table 1, ANOVA analysis).

The contrast between limited space and the presence of a competitor is complemented by the VOLUME analysis, which suggested that different neighbours appropriated space differently (Table 2). Fertility level altered the space available to focal plants for some species combinations but not for others (Table 2).

Only two other studies that the authors are aware of have examined the growth of potentially competing species in pots of different volume. McConnaughay & Bazzaz (in press) found that several species of colonizing annual plants, grown singly without competitors, also increased in biomass as pot volume and fertility increased, although root:shoot ratios were not affected by pot volume in their study. However, they did not compare plants grown alone with those grown in competition. Taylor & Aarssen (1989) grew three hayfield grass species in a replacement-series design at three densities in four pot sizes. Unfortunately the results of that experiment cannot be compared to those of the present study, as all interspecific competitive effects were reported only as yield suppression ratios (YSR) and relative yield totals (RYT).

Conventional indices of competitive ability are typically derived from comparisons of the yield of stands in mixtures with yield in monocultures [e.g. YSR and RYT (Taylor & Aarssen 1989), 'relative yields' (Harper 1977, pp. 267–276), 'aggressivity' (McGilchrist & Trenbath 1971), or performance in mixture as a percentage of that in monoculture (Mitchley & Grubb 1986)]. Austin *et al.* (1985) expressed performance in both monoculture and in mixture for each species relative to the yield of the highest-yielding species. It is difficult to relate the outcome of an experiment expressed in terms of such an index to the results of other experiments, because the results depend strictly on the particular species combination used in each experiment.

While the use of the yield of a stand in monoculture as a basis to assess stand yield in mixture may be appropriate in agriculture (for which replacement series were originally designed), there are two serious problems in using this approach to interpret the results of ecological competition experiments. These problems are common to any version of the above indices. The first problem is that stand yields rather than the performance of individual plants are the units of measure. In seeking to understand the role and impact of competition in nature, one wishes ultimately to determine differences in fitness among competing phenotypes. Individual plant performance may be directly attributable to the fitness of that individual's phenotype. Stand yield, in contrast, has no obvious relationship to fitness, and consequently cannot offer the information that is most needed. The second problem with conventional indices is that performance in mixture is expressed relative to performance in monoculture, thereby confounding intraspecific with interspecific competitive effects. Suppose that species A has identical competitive effects on individuals of species B and C, reducing the growth of each by half. If intraspecific competition among individuals of species B has a greater effect than intraspecific competition among individuals of species C, any such index will lead to the false conclusion that A affects them differently, even if plants of species B and C are the same

size. There is no general reason that intraspecific competitive effects should serve as a 'control' against which interspecific effects are measured; each should be examined independently. For these reasons, in ecological competition experiments, performance should be measured for *individuals* and not stands, and mean yields should be expressed directly (in g dry mass, number of seeds, etc., as in Fig. 1 and the ANOVA analysis) or relative to the potential for growth without competitors (as in the EFFECTS analysis).

Competition and resource level

Competition did not have greater effects at higher fertility levels and when more space was available. Nor were the effects of competition greater at lower fertility and when space was more restricted. There were no apparent trade-offs in competitive abilities at different resource levels. There was a striking lack of pattern in all analyses concerned with detecting increased competitive effects at either high or low levels of available resources (space and nutrients; ANOVA, DEWIT and EFFECTS analyses).

Individual plant mass and root:shoot ratios revealed few significant interactions between neighbour identity and either pot size or fertility level (ANOVA, Figs 1 and 2). (The two exceptions were a possibly reduced competitive effect of *Vicia* on *Achillea* at high fertility, and a greater effect in small than large pots of *Vicia* neighbours on root:shoot ratios in *Vicia* focal plants.)

The DEWIT analyses failed to show any general patterns of competitive reversals or trends in competitive outcome with increased pot size or fertility level (Fig. 3). The EFFECTS analysis showed conclusively that, in this experiment, competitive effects and responses were neither dramatically increased nor decreased as available space and nutrients became more restricted (Table 3). While some studies have shown that the disparity between competitors was greatest at high fertility (e.g. Mahmoud & Grime 1976; Austin & Austin 1980; Parrish & Bazzaz 1982; Zangerl & Bazzaz 1983), others have disputed the generality of that result (e.g. Newbery & Newman 1978).

Intraspecific and interspecific effects

The restriction in an individual plant's growth, for the poorer competitor of a pair, was more severe when its neighbour was of a different species than when the neighbour was a conspecific (DISPARITY index). This supports the interpretation that among competing plants the disparities between individuals of different species are more consequential than the greater resource use overlap of same-species neighbours. Differences in initial advantage (seed size) and inherent differences in growth rate and competitive abilities would be greatest among interspecific pairs.

Among interspecific pairs, the 'losing' member suffered most when available space was most limiting, and performed proportionately better in larger pots. Both the greater effect on neighbours of different species, and the greater reduction in smaller pots suggest that active interference of the larger individual with the smaller may be occurring, particularly for interspecific pairs.

Individual plants did not produce as much biomass as pairs of plants, indicating that even under the high levels of competition created by the experimental treatments, there may have been some differentiation in resource use among members of a pair (TOTAL analysis). At the higher fertility level, interspecific pairs produced more than intraspecific pairs, further suggesting differentiation in resource use among dissimilar plants. (The difference between intra- and interspecific pairs was not realized at the low fertility level.)

The rather surprising inference of partially non-overlapping resource use among competing members of a pair is also supported by the fact that average values for R_s and E_s were greater than 0.50 (EFFECTS analysis).

Plant size and competitive effects

There was a generally consistent hierarchy of competitive superiority that was the same for competitive effects and responses, for the sizes of plants grown without competitors, and for seed sizes at the start of the experiment. Overall, *Vicia*, with the largest seeds, produced the largest plants when grown alone, and had the greatest negative effects on neighbours. *Achillea* had the smallest seeds, the smallest plants, and the least effect on neighbours (ANOVA, VOLUME, DEWIT and EFFECTS analyses). There were, however, departures from this picture which were consistent across analyses. The effects of *Dactylis* neighbours were greater than expected, particularly at higher fertility and in larger pots. In some cases the competitive effects of *Dactylis* were as great as or greater than much larger *Vicia* neighbours. *Dactylis* dominated mixtures in larger pots more effectively than those in smaller pots, and it responded most strongly of the species studied here to an increase in available space, with or without neighbours (Fig. 1).

Miller & Werner (1987), Goldberg & Fleetwood (1987) and others have also found general competitive hierarchies that were consistent with the hierarchy of initial seed size or with mean individual plant size. However, in our study, the ratio of seed masses tended to be much greater than the ratios of final plant masses [compare seed masses (see Analyses of yield individual⁻¹, above) with data in Fig. 1]. This would suggest that inherent differences in growth rate and in competitive ability may overcome initial differences in seed mass. The large disparity in mean seed size between *Vicia* and *Dactylis* ($\times 26$) is greatly diminished, for example, when one compares plant mass even for plants grown singly. Fertilization and competition further diminish this disparity. At pot size 4, when the plants were grown alone, *Vicia* was 2.6 times the mass of *Dactylis* at low fertility, but only 1.5 times its mass at high fertility. When grown together, *Vicia* was only twice the mass of *Dactylis* at low fertility, and almost the equivalent mass ($\times 1.1$) at high fertility. Newbery & Newman (1978) reported congruent results: plants that were initially small grew faster than large ones, and initial disparities in plant sizes were decreased by competition.

Observations on allocation patterns

Root:shoot ratios differed among species, and were strongly influenced not only by substrate fertility and available space, but by the identity of the competing neighbour. Goldberg & Fleetwood (1987) found differences in root:shoot ratios in response to different competitors, but no consistent direction of change. In the present study, means for root:shoot ratio varied most in *Achillea*, the poorest competitor, and were most constant in *Vicia*, generally the best competitor. Austin *et al.* (1985) found that *Carduus nutans*, the species that was most depressed in mixture relative to monoculture, also experienced the greatest shift in root:shoot ratios from monoculture to mixed culture. Similarly, in a study by Zangerl & Bazzaz (1983), root:shoot ratio in a poorer competitor was strongly affected by competition, while that of a superior competitor was not altered by competition. The connection between these factors is unclear, and warrants further investigation. Goldberg & Fleetwood (1987) suggest that the direction of change in allocation may be indicative of the resource for which the species are competing, and it

may be that degree of plasticity of response indicates the extent to which competition for resources is limiting for different species or individuals.

Conclusion

In seeking to understand the mechanisms by which plants compete, it is useful to distinguish two major phases of plant growth. The highly simplified conditions of two plants growing together in a pot may be used as an example. Factors influencing the outcome of the two phases of growth may account for differences among plant species in competitive effects and responses in pots of different sizes. In the first phase, when two seedlings are introduced into or germinate in a pot, each initially grows without being affected by its neighbour. Differences among seedlings in biomass up to the time when interactions commence are due to inherent differences in the ability to acquire (uncontested) resources, and in the ability to convert resources into biomass (including genetic differences, differences in seed size, etc.). In the second phase, the two plants in a pot begin to interact, and a plant's ability to continue to grow depends on the capacity to acquire contested resources (which may or may not differ from the ability to acquire uncontested resources), on the ability to interfere with the other plant's acquisition of resources, and on the plant's susceptibility to interference. All of these factors in both phases of growth are components of plant competitive ability.

The difference between competition in larger and smaller pots may simply be differences in the timing of the commencement of interaction between the plants, but this is not necessarily the case. When competition at two resource levels is compared, plants in more fertile substrate may not only interact sooner, but may be larger when they meet. In addition to differences that occur in the first phase of growth before the plants affect one another, the effects of the interaction between them will also influence final biomass. The experimental and analytical approaches described here separate factors that are usually confounded, offering the opportunity to make comparisons that have not been possible with previous designs. Experiments that expand upon these methods may prove helpful in the exploration of the mechanisms by which plants compete.

Most studies concerned with competition for space have measured the space available to individual plants rather than actually manipulating it (e.g. Silander & Pacala 1985, but see Ross & Harper 1972), confounding the effects of diminished space with those of a greater density of neighbours. This study used conventional and novel analyses and a unique experimental design in an attempt to overcome those problems. Competition for space and resources among plants may be most intense when those commodities are in short supply, as appears to be the case for many animals, or may be most intense when space and resources are abundant and competing neighbours are larger and closer. It is by attempting to distinguish competitive effects and responses (Goldberg & Werner 1983), competition for space and for soil resources, and species-specific differences from size-specific differences, that we may hope to begin to understand the mechanisms and consequences of competition among terrestrial plants.

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REFERENCES

- Austin, M. P. & Austin, B. (1980). Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology*, **68**, 891–918.
- Austin, M. P., Groves, R. H., Fresco, L. M. F. & Kaye, P. E. (1985). Relative growth of six thistle species along a nutrient gradient with multispecies competition. *Journal of Ecology*, **73**, 667–684.
- Connolly, J. (1986). On difficulties with replacement-series methodology in mixture experiments. *Journal of Applied Ecology*, **23**, 125–137.
- Goldberg, D. E. (1987). Neighborhood competition in an old-field plant community. *Ecology*, **68**, 1211–1223.
- Goldberg, D. E. & Fleetwood, L. (1987). Competitive effect and response in four annual plants. *Journal of Ecology*, **75**, 1131–1143.
- Goldberg, D. E. & Werner, P. A. (1983). Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *American Journal of Botany*, **70**, 1098–1104.
- Gurevitch, J. & Unnasch, R. S. (1989). Experimental removal of a dominant species at two levels of soil fertility. *Canadian Journal of Botany*, **67**, 3470–3477.
- Harper, J. L. (1977). *Population Biology of Plants*. Academic Press, New York.
- Inouye, R. S. & Schaffer, W. M. (1981). On the ecological meaning of ratio (de Wit) diagrams in plant ecology. *Ecology*, **62**, 1679–1681.
- Jolliffe, P. A., Minjas, A. N. & Runeckles, V. C. (1984). A reinterpretation of yield relationships in replacement series experiments. *Journal of Applied Ecology*, **21**, 227–243.
- McConnaughay, K. D. M. & Bazzaz, F. A. (1990). Physical space as a resource: the performance of colonizing annuals in relation to soil volume. *Ecology* (in press).
- McGilchrist, C. A. & Trenbath, B. R. (1971). A revised analysis of plant competition experiments. *Biometrics*, **27**, 659–671.
- Mack, R. N. & Harper, J. L. (1977). Interference in dune annuals: spatial patterns and neighbourhood effects. *Journal of Ecology*, **65**, 345–364.
- Mahmoud, A. & Grime, J. P. (1976). An analysis of competitive ability in three perennial grasses. *New Phytologist*, **77**, 431–435.
- 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.
- Mitchley, J. & Grubb, P. J. (1986). Control of relative abundance of perennials in chalk grassland in southern England. I. Constancy of rank order and results of pot- and field-experiments on the role of interference. *Journal of Ecology*, **74**, 1139–1166.
- Mithen, R., Harper, J. L. & Weiner, J. (1984). Growth and mortality of individual plants as a function of 'available area'. *Oecologia*, **62**, 57–60.
- Newbery, D. McC. & Newman, E. I. (1978). Competition between grassland plants of different initial sizes. *Oecologia*, **33**, 361–380.
- Parrish, J. A. D. & Bazzaz, F. A. (1982). Competitive interactions in plant communities of different successional ages. *Ecology*, **63**, 314–320.
- Ross, M. A. & Harper, J. L. (1972). Occupation of biological space during seedling establishment. *Journal of Ecology*, **60**, 77–88.
- Silander, J. A. Jr & Pacala, S. W. (1985). Neighborhood predictors of plant performance. *Oecologia*, **66**, 256–263.
- Taylor, D. R. & Aarssen, L. W. (1989). On the density dependence of replacement series competition experiments. *Journal of Ecology*, **77**, 975–988.
- Trenbath, B. R. (1974). Neighbour affects in the genus *Avena*. II. Comparison of weed species. *Journal of Applied Ecology*, **11**, 111–125.
- Weiner, J. (1982). A neighborhood model of annual plant interference. *Ecology*, **63**, 1237–1241.
- Zangerl, A. R. & Bazzaz, F. A. (1983). Responses of an early and a late successional species of *Polygonum* to variations in resource availability. *Oecologia*, **56**, 397–404.

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