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COMPETITIVE EFFECTS AND RESPONSES BETWEEN PLANT SPECIES IN A FIRST-YEAR OLD-FIELD COMMUNITY'

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Abstract. Competitive interactions involve two separate processes: the effect of a species on others in the community and the response of a species to all others. Five species from a 1st-yr field were investigated to determine if there is any correlation between competitive effect and response and if the patterns of effect and response can explain the relative success of each species in the full community. Effect and response were measured by observing the growth of individuals in all possible monocultures and two-species mixtures, using ambient densities (Year 1) and a range of densities (Year 2) for each species. Both monocultures and two-species mixtures were obtained by removing unwanted individuals at emergence, leaving naturally emerging individuals of the desired species.

Competitive effect and response were found to be inversely correlated. The inverse correlation lead to a hierarchy of competitive ability, with *Ambrosia artemisiifolia* being the competitive dominant, followed by *Agropyron repens*, *Plantago lanceolata*, and finally the competitive subordinates *Chenopodium album*, *Lepidium campestre* (used in Year 1), and *Trifolium repens* (used in Year 2). The interactions were generally asymmetric, e.g., *Ambrosia artemisiifolia* had a large suppressive effect on the other species and demonstrated no response to their presence. The hierarchy and a lack of specificity of the interactions suggest that all the species are limited by, and competing for, the same resource or resources. The hierarchy of competitive ability appears to be a major factor in determining the abundance of each species in the full community.

Key words: Agropyron repens; Ambrosia artemisiifolia; Chenopodium album; community structure; competition; competitive hierarchy; interspecific interactions; Lepidium campestre; old field; Plantago lanceolata; Trifolium repens.

INTRODUCTION

The ability of a species to persist and prosper in a community is often determined by its competitive interactions with other species (Connell 1983, Schoener 1983). These competitive interactions involve two separate processes: the effect of a species on others in the community and the response of a species to all others in the community. Successful species must have either a low response to the abundance of other species and/ or such a large effect that the abundance of other species is greatly reduced. Conceivably, a particular species may have a low response and a high effect, or any other combination of effect and response.

Patterns in the competitive effect and competitive response of the species in a given community may not only explain the relative abundance of each species but may also provide some insight into the nature of the forces that structure the community. For example, a

² Present address: Barnes Laboratory, Department of Biology, University of Chicago, Chicago, Illinois 60637 USA. species that has little effect on and response to other species in the community is probably not limited by the same resources and will not be affected by changes in the abundances of other species in the community. Pairs of species which have both a large competitive effect on and a large competitive response to one another probably use, and are limited by, the same resources. Alternatively, pairs of species in which one has a large competitive effect on, but little competitive response to, the other show an asymmetric competitive ability in using some common resource (Aarssen 1983).

Patterns of competitive effect and response are particularly interesting in plant communities because of the nature of plant resources. Previous work in theoretical ecology and animal community structure proposed that individual species must have some exclusive use of resources to be able to persist in the community (e.g., May and MacArthur 1972, May 1973; for plants, Van den Bergh and Braakehekke 1978). This leads to species in the same community occupying different "niches," the niche being the set of all biotic and abiotic factors controlling the distribution and abundance of a species. However, all plants have very similar resource requirements, each individual requiring light, water, CO_2 , and a limited number of crucial nutrients. Because of this, several authors have argued

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TABLE 1.	Species abundances in Bailey Front	Yard for Years	1 (1982) and 2 (1	1983). Mean ind	lividual dry	mass (M) , yields
of abor	veground dry biomass (Y), and speci	es densities (D) were measured	in September o	of each year.	. Only yield was
determ	ined for the rhizomatous grasses.					

	Year 1 (1982)			Year 2 (1983)			
	M (g)	<i>Y</i> (g/m ²)	D (no./m ²)	M (g)	<i>Y</i> (g/m ²)	D (no./m²)	
Ambrosia artemisiifolia L.	1.53	137.17	89.8	1.60	140.55	88.0	
Agropyron repens (L.) Beauv.		36.85			50.10		
Plantago lanceolata L.	0.87	32.07	36.9	0.45	11.79	26.0	
Chenopodium album L.	0.06	2.56	45.3	0.07	8.80	126.0	
Lepidium campestre (L.) R. Br.	0.05	1.96	40.4	0.08	1.38	15.4	
Trifolium repens L.	0.16	18.64	113.3	0.06	2.36	38.0	
All other species		22.37	•••	•••	19.85		

that this niche diversification hypothesis is not applicable to plant communities (e.g., Silander 1976, Connell 1978, Huston 1979, Newman 1982, Goldberg and Werner 1983).

Because of their sessile nature, there is also a strong spatial component to competition between plants. Both distances between individuals (e.g., Mack and Harper 1977, Weiner 1982, Watkinson et al. 1983) as well as differences in growth form and sizes (e.g., Givnish 1982) will strongly influence the competitive effects and responses of species in a plant community.

In this study, we investigated the competitive effects and responses of the five dominant plant species in a simple weedy plant community. Field experiments were designed to: (1) determine if some correlation or pattern existed between the competitive effects and responses of species in this community, and (2) relate the effect and response of each species to its relative abundance and growth in the full community, both within and between two seasons.

MATERIALS AND METHODS

Experiments on plant interactions were performed in 1982 (Year 1) and 1983 (Year 2). The experimental design consisted of plots containing different combinations of five species. The design was similar in both years, but differed in the number and size of replicates and in that several additional treatments were used in the 2nd yr.

Field site. — The plant community studied was located in Bailey Front Yard, a periodically plowed site at the W. K. Kellogg Biological Station in Kalamazoo County, Michigan. The soil is a sandy Kalamazoo loam that is moderately acidic (pH 5.9) and relatively infertile (organic matter 1.6%, total N 0.9 mg/kg, PO₄ 14.8 mg/kg, K 135.5 mg/kg). The field had been sprayed with the herbicide Roundup in 1979, 3 yr before this study began.

Plant community.—The 1st-yr community contained > 30 plant species, most of which were very rare and individually contributed very little to the total autumn biomass in the field. The large majority of these species were weedy annuals and short-lived perennials, although seedlings of invading tree species were found occasionally.

In each of the 2 yr of the study, five species made up >90% of the biomass of the communities (Table 1). Three species were co-dominants in biomass or yield: *Ambrosia artemisiifolia, Agropyron repens*, and *Plantago lanceolata*; a fourth species, *Chenopodium album*, had very high numbers of individuals in both years. The choice of the fifth species was different for the 2 yr of the study because of variation in the abundances of minor species from year to year (1st yr, *Lepidium campestre*; 2nd yr, *Trifolium repens*). These species were selected for the experiment and all others were removed in each year of the study.

The six species have different life histories and growth forms. Ambrosia artemisiifolia, common ragweed, and Chenopodium album, lambsquarters, are upright annuals; Lepidium campestre, field cress, is a rosetteforming annual; Plantago lanceolata, narrow-leaved plantain, is a rosette-forming perennial; Trifolium repens, white clover, is a creeping perennial; Agropyron repens, quackgrass, is perennial and the only grass species. In Bailey Front Yard, Agropyron was also the only species that emerged in the spring from rhizomes formed in the previous year. Individuals of all other species emerged from seed in each year of the study. The six species have very similar phenologies, all emerging in the spring, flowering, and setting seed (if individuals achieve a large enough size), and senescing in the autumn at approximately the same time.

Field methods and design.—For each year of the study, the experimental area in Bailey Front Yard was plowed to a depth of 20 cm in November of the previous year and smoothed with a York rake in the following March. Square quadrats, either 2×2 m or 1.3×1.3 m, were marked out in April prior to seedling emergence. Each quadrat was randomly assigned a single treatment consisting of either a monoculture or two-species mixture at various densities.

Following emergence in late April and early May, all undesired species from each quadrat were removed. Removal of seedlings was performed by hand, gently pulling each individual from the moist soil. This re-

moved the root, preventing regrowth, and did not significantly disturb the soil surface. Rhizomatous grasses (e.g., Agropyron repens and Bromus inermis) could not be removed in this way without soil disturbance, so they were removed by continuous clipping at the soil surface throughout the growing season of Year 1. Most culms did not resprout after two or three clippings. In Year 2, a weak (3%) solution of a contact herbicide, Roundup (the isopropylamine salt of glyphosate), was applied to individual culms of grass using a small sponge in early May and again in early June. This treatment was quite effective in removing all undesired rhizomatous grasses for the remainder of the year and appeared to have no effect on other individuals in the quadrats. The quadrats were monitored throughout each summer and weeded as necessary to prevent reinvasion of undesired species.

Densities of desired species were also controlled. Low densities consisted of one-half the natural or ambient densities, and were maintained using the methods described above. High densities were greater than double the ambient densities and were produced by deliberate seeding of quadrats with the desired species in early April. Seeds were obtained from resident populations in the previous autumn.

The 2 yr of the experiment differed in the number of replicates and the types of treatments. In Year 1 (1982), 312×2 m quadrats were used, with treatments randomly assigned to each quadrat. Each species was at its ambient density either as a monoculture or paired with another species, with each unique combination of species and density in either two or three replicate quadrats. In Year 2, the project was greatly expanded with 202 1.3 \times 1.3 m quadrats marked out in a randomized block design, with each species being either completely absent, at half-ambient density, at full ambient density, or at a high density, each unique combination found in a minimum of five replicate quadrats. In the half-densities, the fate of each individual plant in a quadrat was determined by a coin toss and the plant was either left alone or removed as described above.

In midsummer (July 25 in Year 1 and July 11-15 in Year 2), 10 plants of each species, growing within the center 1 m² of each quadrat, were measured to estimate treatment effects. Nondestructive morphological measures were used, different for each species: for Ambrosia artemisiifolia and Chenopodium album, height and length of longest leaf; for Plantago lanceolata and Lepidium campestre, number of leaves; for Trifolium repens, number of main branches and length of longest branch. At the same time, correlates of these measures with total dry biomass were determined using 30 individuals of each species from nearby nonexperimental areas. These individuals were measured as above and then aboveground portions were harvested, dried at 65°C for 72 h, and weighed to obtain ovendried biomass. Multiple regression was used to determine morphology-biomass relationships, which were then used to estimate the biomasses of the plants in the experimental quadrats. For *Agropyron repens*, there was no statistically satisfactory measure that estimated biomass and so there were no midsummer estimates of biomass for this species.

Plant survival was followed in Year 2 for all the study species except *Agropyron*. In *Agropyron*, the rhizomatous habit precludes identification of individual genets. At the time of the initial weeding, most, if not all, of the individuals of the study species had emerged (Miller 1987) and were still in the cotyledon or firstleaf stage. The individuals of each species were counted in the center 0.6×0.6 m of each plot and again when plants were harvested in September. The two densities were used to estimate the survival of individuals of each species in each quadrat.

In each year, all plots were harvested during the last week of September and the first week of October. Only the center 1 m² was harvested in Year 1 and center 0.6 m² in Year 2. Each individual plant was clipped at ground level, pressed, dried for 72 h at 65°, and then weighed to determine aboveground biomass.

The species interactions at natural densities were analyzed as an incomplete mixture diallel (see Trenbath 1977). The mean biomass of individuals in each mixture can be expressed as a proportion of plant biomass in monoculture and arranged in a matrix form. Each matrix value Y_{ij} is the mean biomass of species *i* when grown with species *j*, divided by the growth of species *i* in monoculture. The mean of the values in row *i* is defined as the mean response of species *i*, while the mean of the values in column *j* gives the mean effect of species *j*. Mean effect and response are similar to species or producer effect and associate effect, respectively (McGilchrist 1965, Trenbath 1977, Moore and Williams 1983).

RESULTS

Species interactions at natural densities

The experimental design allowed a comparison of growth and survivorship of each species when in monoculture and when growing with each of the other species. The species had rather different patterns of effect on and response to other species. These patterns of effect and response were remarkably consistent between the 2 yr of the study and between midsummer and autumn.

Year 1. — Ambrosia demonstrated no statistically significant response when grown with other species, growing almost as well with each associate species as it did in monoculture (Table 2). In contrast, Agropyron was significantly suppressed when grown with different associate species. In monoculture, Agropyron reached a yield of 169 g/m² but it never achieved >55% of this yield when grown with Ambrosia or Plantago (Table 2). Plantago was also significantly suppressed (P < .05, Table 2) when grown with other species, particularly when grown with Ambrosia or Agropyron. In the pres-

TABLE 2.	Response of focal s	species to the	presence of	associate sp	pecies. Values	s are express	sed as a pr	oportion (of growth	in
monocu	lture (the principal	diagonal).*								

		A	ssociate specie	s		Mean dry mass in	Maan
Focal species	Ambr	Agro	Plan	Lepid	Chen	(g)	response
Year 1, midsummer							
Ambrosia Agropyron	1.00ª	0.58ª	1.00ª	0.64ª	1.00ª	1.9	0.80
Plantago Lepidium Chenopodium	0.20ª 0.04ª 0.07ª	0.57 ^{ab} 0.06 ^a 0.25 ^a	1.00 ^b 0.91 ^{ab} 0.24 ^a	0.95 ^ь 1.00 ^ь 1.14ª	0.92 ^b 1.23 ^b 1.00 ^a	5.8 3.3 1.4	0.66 0.56 0.43
Mean effect	0.10	0.37	0.72	0.91	1.05		
Year 1, autumn							
Ambrosia Agropyron Plantago Lepidium Chenopodium Mean effect	$\begin{array}{c} 1.00^{a} \\ 0.55^{ab} \\ 0.19^{a} \\ 0.12^{a} \\ 0.06^{a} \\ 0.23 \end{array}$	$\begin{array}{c} 0.62^{a} \\ 1.00^{b} \\ 0.61^{b} \\ 0.26^{a} \\ 0.19^{a} \\ 0.42 \end{array}$	$\begin{array}{c} 0.86^{a} \\ 0.51^{a} \\ 1.00^{b} \\ 0.54^{ab} \\ 0.33^{ab} \\ 0.56 \end{array}$	$\begin{array}{c} 0.67^{a} \\ 0.86^{ab} \\ 1.06^{b} \\ 1.00^{bc} \\ 1.46^{b} \\ 1.01 \end{array}$	0.93 ^a 0.97 ^b 1.06 ^b 1.76 ^c 1.00 ^b 1.18	3.8 169† 6.2 1.0 1.2	0.77 0.72 0.73 0.67 0.51
		Associate	e species			Mean dry mass in monoculture	Mean
Focal species	Ambr	Agro	Plan	Trif	Chen	(g)	response
Year 2, midsummer				······································		·····	
Ambrosia Agropyron	1.00ª	0.91ª	0.86ª	0.75ª	0.88ª	1.2	0.85
Plantago Trifolium Chenopodium Mean effect	0.22ª 0.17ª 0.27ª 0.22	0.21 ^a 0.20 ^a 0.28 ^a 0.40	1.00^{b} 0.34^{ab} 0.41^{a} 0.54	0.68^{b} 1.00^{b} 0.49^{a} 0.64	0.66 ^b 0.94 ^b 1.00 ^a 0.82	2.8 3.3 1.4	0.44 0.41 0.36
Year 2, autumn							
Ambrosia Agropyron Plantago Trifolium Chenopodium Mean effect	$\begin{array}{c} 1.00^{a} \\ 0.37^{a} \\ 0.23^{a} \\ 0.22^{a} \\ 0.08^{a} \\ 0.22 \end{array}$	$\begin{array}{c} 0.94^{a} \\ 1.00^{b} \\ 0.36^{a} \\ 0.27^{a} \\ 0.16^{ab} \\ 0.43 \end{array}$	1.03 ^a 0.86 ^b 1.00 ^b 0.67 ^b 0.43 ^{bc} 0.75	1.02 ^a 0.95 ^b 1.08 ^b 1.00 ^b 1.15 ^c 1.05	$\begin{array}{c} 1.04^{a} \\ 1.16^{b} \\ 0.73^{b} \\ 0.90^{b} \\ 1.00^{c} \\ 0.96 \end{array}$	4.2 155† 2.5 0.5 2.2	$ 1.01 \\ 0.84 \\ 0.60 \\ 0.51 \\ 0.46 $

* Values in the same row followed by different letters are significantly different at the P < .05 level (Year 1, GT2 Test: Sokal and Rohlf 1981:245; Year 2, Welsch Step-up Procedure: Sokal and Rohlf 1981:253).

 \dagger Yield, measured in g/m².

ence of *Ambrosia*, *Plantago* achieved < 20% of the size it exhibited in monoculture. *Plantago* had no response to the presence of *Chenopodium* and *Lepidium*. Both *Lepidium* and *Chenopodium* were very strongly suppressed in the presence of *Ambrosia* or *Agropyron* and were also somewhat suppressed in the presence of *Plantago*. In probably the most extreme example of competitive suppression noted, *Lepidium* in the presence of *Ambrosia* had < 4% of the growth it achieved in monoculture.

Looking at the same data for patterns of the effect of each species on others, it is apparent that *Ambrosia* always had a strong suppressive effect on the growth of other species (Table 2). *Agropyron* and *Plantago* significantly suppressed the growth of all species but *Ambrosia. Lepidium* and *Chenopodium* had no significant effect on the growth of any other species.

Year 2.—The mean growth of individuals of the five species in Year 2 also showed very different patterns

of competitive effect and response by the various species, consistent with Year 1. The pattern exhibited by any particular species was consistent between midsummer and autumn. The growth of Ambrosia was not affected by the presence of any other species. Whether individuals of Ambrosia grew in monocultures or with other species, they always averaged ≈ 1.0 g/individual at midsummer and slightly over 4.0 g/individual at the autumn harvest (Table 2). The growth of Agropyron was affected only by the presence of Ambrosia, which reduced the yield of Agropyron by 63% (Table 2). Growth of Plantago was reduced only by Ambrosia and Agropyron, which suppressed the growth of individuals of *Plantago* to <40% of the growth shown in monoculture. The growth of Trifolium, the species that was used in place of Lepidium in Year 2, also was suppressed in the presence of Ambrosia and Agropyron and, to a lesser degree, *Plantago*. *Chenopodium* had no significant response to the presence of any other species As in Year 1, *Ambrosia* had the greatest effect on other species, reducing their growth to a mean of 22% of the size achieved in monocultures (Table 2). *Agropyron* had somewhat less effect, as did *Plantago* (mean effects of 43 and 75%, respectively, of the size achieved by each species in monoculture; Table 2). The presence of *Trifolium* or *Chenopodium* had no effect on the growth of any other species.

The most extreme effect of competition would result in the death of the affected species. Survivorship was measured in the 2nd yr, and there was little or no mortality in *Ambrosia*, *Plantago*, and *Chenopodium* either in monoculture or in mixture (Table 3). *Trifolium* did exhibit a significant reduction in survival when grown with *Ambrosia* or *Agropyron* (74 and 59% survival, respectively). We were unable to determine survivorship of genets of *Agropyron*; however, no individual shoots of this species were observed to die in any plot during the study.

Thus, 2 yr data indicated that there were very strong and consistent differences in the competitive effects of associate species (Table 2). *Ambrosia* always had the greatest competitive effect on each of the other species, reducing the growth of other species to $\approx 23\%$ of their growth in monocultures. *Chenopodium* and *Lepidium* (Year 1) or *Chenopodium* and *Trifolium* (Year 2) had the least effect, if any, on the different focal species, never reducing the growth of other species by a significant amount.

There were also large differences in the average responses or sensitivities of the various species to competitive effects (Table 2). *Ambrosia* was never significantly affected by the presence of any of the associate species, while the populations of *Chenopodium* and *Lepidium* (Year 1) or *Chenopodium* and *Trifolium* (Year 2) were on average suppressed to $\approx 50\%$ of their growth in monoculture. This ranking or hierarchy of competitive response was also very consistent and the exact opposite of the hierarchy of competitive effect.

If high competitive ability is determined by some combination of a large competitive effect on other species but little response to the presence of other species, then the combined rankings of mean effect and response (Table 2) lead to a consistent ranking of competitive ability:

Ambrosia > Agropyron > Plantago > Chenopodium = Lepidium = Trifolium.

So, competitive ability seems to be a transitive property of these populations. Note that this ranking is similar to the ranking of mean individual plant size (Table 1). It is tempting to infer that size confers competitive effect: however, it must be remembered that

TABLE 3. Proportion of focal individuals in Year 2 surviving when grown in combination with different associate species. The principal diagonal gives the survivorship in monocultures.*

Focal	Associate species						
species	Ambr	Agro	Plan	Trif	Chen		
Ambrosia	1.00ª	1.00ª	1.00ª	1.00ª	1.00ª		
Agropyron Plantago	1.00ª	1.00ª	1.00ª	1.00ª	1.00ª		
Trifolium Chenopodium	0.74 ^{ab} 1.00 ^a	0.59ª 1.00ª	0.93 ^{bc} 0.97ª	1.00° 0.89ª	0.97 ^{bc} 1.00ª		

* Values in the same row followed by different letters are significantly different (P < .05, Welsch Step-up Procedure: Sokal and Rohlf 1981:253).

[†] The survival of *Agropyron* could not be determined in the field.

plant size may be as much an indicator of competitive response as of effect.

The experiments above measured species interactions at the single, natural density of each associate species. In some other habitat, with different resource levels or ambient densities, competitive outcomes might be different. In the 2nd yr of the study, the densities of species were varied in both monocultures and twospecies mixtures to further understand how competitive abilities are affected by species abundance.

Species interactions over a range of densities

To obtain a measure of competitive effects as a function of competition density, experiments in Year 2 were performed in which the abundances of species were varied in both monocultures and two-species mixtures.

Monocultures.—In monocultures, individual performance showed a significant negative response to an increasing density of conspecifics for all five species (Fig. 1). There were differences, however, in the shapes of the response curves and variations around the curves.

The relationship between density and mean plant biomass was strongly nonlinear for four of the species. Ambrosia and Trifolium were both suppressed at high densities, the reciprocal of mean mass adequately described as a linear function of density (reciprocal $r^2 =$ 0.74 and 0.45, respectively, P < .05; compared with linear $r^2 = 0.36$ and 0.34). Plantago and Chenopodium exhibited an even more strongly nonlinear relationship, best described for both species by a log-log curve $(R^2 = 0.75 \text{ and } 0.85, \text{ respectively}, P < .05; \text{ linear } r^2 =$ 0.38 and 0.46). We were able to obtain very high densities of Plantago and Chenopodium through successful seeding, and it may be that the degree of curvature to the relationship was simply a function of the amount of the asymptotic portion of the curve we were able to measure.

The negative relationship between the growth of Agropyron and density was barely significant at the P < .05 level. This reflects a problem associated with pe-



MONOCULTURE DENSITY (individuals/m²)

FIG. 1. The mean biomass of each of the five species when grown in monocultures at various densities in Year 2.

rennial rhizomatous grasses. It is very difficult to determine the actual density or biomass of genetic individuals because of underground connections. We estimated densities and mean plant biomass of *Agropyron* by treating culms as individual plant (Fig. 1), but this overestimated the actual density and underestimated the mass of genetic individuals. In spite of biases in the opposite direction, there was still a negative relationship, suggesting that competitive interactions do limit the growth of this species in monocultures.

Two-species mixtures.—It is very difficult to quantify interspecific effects independently of the intraspecific effects also usually present. Instead of eliminating the intraspecific effect, we attempted to hold it constant by maintaining the density of the focal species at a single value and then measuring the effect of various densities of the associate species (additive design: Harper 1977: 249). In Year 2, each unique pair of species was maintained in 15 plots, 10 of which contained the focal species at the ambient density. These 10 plots were used to determine the response of the focal species to the yield (dry biomass per square metre) of each of the different associate species. Five of these plots contained the associate species at the ambient density and five contained the associate species at half-ambient densities. Because the variance in intraspecific effects is included in the error variance of the regressions, this additive design restricts rather than eliminates variance in the intraspecific effects.

The response (biomass) of individuals of the focal species to varying the yield of an associate species was generally negative (competitive) or near zero (Table 4). However, this response was statistically significant in



YIELD OF ASSOCIATE SPECIES (g/m²)

FIG. 2. The mean biomass of each species as a focal species when grown in pairwise combinations in Year 2 with each of the other species at various yields. Each letter indicates the yield of a specific associate species: A = Ambrosia artemisiifolia, G = Agropyron repens, P = Plantago lanceolata, T = Trifolium repens, and C = Chenopodium album.

only 4 of the 20 possible combinations. The growth of individuals of Ambrosia was not significantly affected by the biomass of any of the associate species, the same effect demonstrated by the experiments at constant densities. Conversely, varying the yield of Ambrosia had virtually no effect on the growth of the other species. This was unexpected, as the previous comparison of the growth of individuals of all other species with and without Ambrosia (Table 2) indicated that Ambrosia usually strongly suppressed their growth. However, the biomass values of Ambrosia used in the regression analysis were relatively high because even at low densities Ambrosia produced high yields. So, over the range of yields investigated, any increase in yield did not increase the already large competitive effect that Ambrosia had on other species, because the function describing the effect of Ambrosia yield on growth asymptotically approached zero growth.

Agropyron also did not respond to changes in the yield of any associate species (Fig. 2, Table 4). Its effect on other species was significant, however. Increases in the yield of Agropyron significantly decreased the growth of *Plantago*, *Trifolium*, and *Chenopodium* (Table 4). This is in general agreement with the hierarchy of competitive ability previously discussed.

The growth of *Plantago* responded only to changes in the biomass of *Agropyron*. As discussed above, *Ambrosia* appeared to have a large effect on the growth of *Plantago*, but the magnitude of this effect did not change significantly over the range of yield of *Ambrosia* used in this study (Fig. 2). Increasing yields of *Plantago* did significantly reduce the growth of *Chenopodium*, but had no effect on the other three species (Table 4).

Both *Trifolium* and *Chenopodium* responded negatively to increasing biomasses of other species (Fig. 2). Neither *Trifolium* nor *Chenopodium* had a significant

TABLE 4. Linear correlations between mean dry mass of focal species and the yield of different associate species in two-species mixtures. N = 10 for all species pairs.

Focal	Associate species							
species	Ambr	Agro	Plan	Trif	Chen			
Ambrosia		-0.35	-0.57	0.04	0.32			
Agropyron	0.02	_	0.40	-0.03	0.06			
Plantago	-0.15	-0.65*	_	0.49	0.06			
Trifolium	-0.43	-0.65*	0.00	_	0.01			
Chenopodium	0.22	-0.60*	-0.77**	-0.14	_			

* Significant at P < .05; ** significant at P < .01; a dash indicates that the correlation was not determinated for that situation.

effect on the growth of any focal species, at least at the yields obtained for these two species as associates. The general competitive ability determined for these two species was similar to that found in the experiments at constant densities: both species had little effect on any focal species and were often strongly suppressed by the presence of associates.

The results shown in Fig. 2 demonstrate an interesting pattern. The points for the response of a focal species to the various associate species seem to fall along the same curve. The effects of two different associates at the same biomass are approximately equal. This suggests that the associate species are equivalent in their per-unit-biomass effect on these focal species (see Goldberg and Werner 1983).

However, the data were quite variable, particularly at low abundances of associate species. To best test whether the different associate species were indeed equivalent on a per-unit-biomass basis, we compared the competitive effects of two different associate species over the same range of associate biomass using analysis of covariance (Goldberg and Werner 1983). But, because of the differences in biomass achieved by different associate species regardless of densities, it was very difficult to obtain sufficient overlaps in the ranges of several of the species. For example, we cannot use analysis of covariance to compare the effect of Trifolium and Ambrosia on Chenopodium, because individuals of Trifolium are quite small relative to individuals of Ambrosia, making it impossible to obtain mixtures of each of these species covering the same range of associate yield (Fig. 2).

The correct statistical analysis was possible for only one case: a comparison of the effects of *Agropyron* and *Plantago* on the growth of *Chenopodium*. The per-unitbiomass effects were not significantly different (F =1.2668, P > .28). A second, much less precise way to test for differences in per-unit-biomass competitive effects is a *t* test to compare the effects of two associate species on single focal species over a small range of yield that is common to both associate species. There was sufficient overlap of ranges of two associate species on a focal species to perform this test in 14 of the 30 possible cases (six pairwise combinations of associates for each of five possible associate species). Of these 14 cases, two demonstrated significant differences at P < .05 (14% of the cases). Significant differences in species effects were found between the effects of *Agropyron* and *Chenopodium* on both *Plantago* and *Trifolium*. It is likely that, even at the highest yield attained by *Chenopodium*, it had very little effect on any focal species.

The relationship between associate species yield, regardless of identity and the growth of focal species (Fig. 2) was either nonsignificant (for *Ambrosia* and *Agropyron*) or nonlinear. The relationship for *Plantago*, *Trifolium*, and *Chenopodium* was well described as a linear function between log mean biomass of focal species and log yield of associate species ($r^2 = 0.40$, 0.26, and 0.55, respectively; n = 40 and P < .01 in all cases). This nonlinear relationship between the growth of individuals and the abundance of competitors was also noted in the monocultures discussed above.

DISCUSSION

The two separate components of competitive ability, effect and response, were inversely correlated in the species found in this weedy plant community. This correlation indicates that species interactions were generally asymmetric. That is, there were usually definite "winners" and "losers" between any pair of species. The competitive hierarchy and the asymmetric interactions found in this study suggest that there was some sort of ordered access to the limiting resource or resources (e.g., Watkinson et al. 1983). It would seem that light, especially, could lead to ordered access because of the potential for tall individuals or species to control the resource. The tallest plant may use the resource freely, unimpeded by other plants, the second tallest plant may use the light that filters through to it, unimpeded by those beneath, and so forth. In this simple scenario, the ordered access to light would lead to completely asymmetric interactions and to a hierarchy of competitive effect, as noted in this community. It would seem that some plant resources would bring about a more symmetric or evenly balanced competition between individuals (especially underground resources), while others would be less likely to do so.

In support of this, our study revealed little specificity of species interactions; e.g., *Ambrosia* affected all other species strongly, not just some of them. There was no evidence that any species was specializing to use different resources or classes of resources or, further, that any species might be partitioning the resources used in growth (i.e., water, light, or nutrients). Of course, this does not address the possibility that other niche dimensions were being partitioned. Plants may partition many aspects of the biotic or abiotic environment other than light, moisture and nutrients, such as different microsites or phenologies (Grubb 1977).

Further, the competitive hierarchy was correlated with the ranking of both species yield (grams dry bio-

mass per square metre) and mean size (grams per individual) obtained by each species in the five-species community. For instance, *Ambrosia*, the species with the largest competitive effect, and the least response in two-species experiments, was also the largest and highest yielding species in the five-species community (Table 1). *Chenopodium, Trifolium,* and *Lepidium* were the competitive subordinates and were the smallest, lowest yielding species in the community. So, it appears that competitive ability will, in large part, determine the growth and abundance of each species in the community.

The patterns of species effect and response in this community were very consistent. The hierarchy of competitive ability was very similar in the two sampling periods each year (midsummer and autumn; Table 2), suggesting that the competitive interactions between the species were firmly established before the midsummer dates in both years. The hierarchy was also very consistent between the 2 yr, despite the large differences in the mean biomass of each species. This suggests that the competitive mechanisms or processes did not significantly differ in the 2 yr.

Although consistent hierarchies of the competitive abilities of different species have been found in other studies (Pemadasa and Lovell 1974, Pemadasa 1976, Handel 1978, Fowler 1982; however, see discussion of Williams 1962 in Trenbath 1977), there are presently too few studies to conclude that hierarchies are a general phenomenon or to what extent they might be correlated with resource patterns.

Response.—What determines the competitive response of a species? The shape of the response curve of individuals of each species to an increasing abundance of competitors was generally concave, with the effect of increasing the abundance of competitors asymptotically approaching zero. This response curve was exhibited by species both in monoculture and in two-species mixtures (Figs. 1 and 2).

We suggest that there are at least two possible reasons for this nonlinear relationship. It may simply be that a constant increase in the biomass of competitors does not translate into a constant decrease in the amount of limiting resources available to focal individuals. In other words, biomass of competitors has a nonlinear effect on the amount of resources available to a focal individual.

Or, the nonlinear response curve may be a result of temporal patterns of competition. When the seedlings first emerge from the ground in late April and early May, they generally do not overlap spatially because of their small size. At this time, there are few competitive interactions. As these individuals grow, occupying more space and requiring a greater amount of resources, the intensity of competition increases. Thus, the time when effects of neighbors first occurs could vary with density. A nonlinear curve may reflect the fact that, at low densities, the focal individuals have few competitors and are able to achieve some exponential growth before encountering neighboring (competing) plants. As the number of neighbors or competitors is increased, then the lower the probability of having any period of unimpeded growth.

The nonlinear growth curve has interesting implications for the species occurring in the full multispecies community. It suggests that the growth of *Plantago*, *Chenopodium*, *Trifolium*, and *Lepidium* was little affected by the biomass of *Ambrosia* past ~200 g/m². For this reason, it may be difficult to detect the presence of any competitive response of these species to *Ambrosia* by varying the abundance of *Ambrosia*, even though the simple presence of *Ambrosia* has a very great competitive effect. This experimental problem of working with concave response curves was also noted by Schoener (1983).

Effect. - These two-species experiments support at least a general equivalence of competitive effects of different associate species at any yield. All species but Chenopodium appeared to have the same per-unit-biomass effect on focal species. A similar general equivalence of competitive effects was found by Peart (1982) in grassland plant communities and by Goldberg (1987) in a midsuccessional old-field community. Goldberg and Werner (1983) have argued that one would expect to find a general equivalence within growth forms because of these qualities of plants: (1) required resources are qualitatively identical, (2) competitive interactions are mainly diffuse, and (3) size generally confers competitive superiority. Certainly, the plant community in this study seemed to meet these conditions. There appeared to be very little specificity of interactions, individuals of various species appeared to be randomly distributed spatially, resulting in diffuse competitive interactions, and the hierarchy of competitive effects was similar to the hierarchy of mean individual size.

We have only discussed patterns in aboveground biomass. Inclusion of belowground biomass would change the quantitative results since species vary in shoot/root ratios and in how shoot/root ratios vary with density (Harper 1977:362). However, including the belowground biomass would probably not affect the hierarchies of competitive effect and response, because the hierarchies are based on the ratios of mean plant biomass in mixture/mean plant biomass in monoculture. Addition of belowground biomass would also probably not change the ranking of mean species biomass in any significant way (Table 1). It should be noted that several of the species used have been reported as being allelopathic to varying degrees (e.g., Jackson and Willemsen 1976, Harper 1977:373). However, the evidence for allelopathy is not conclusive and no indication of allelopathic effects were noted in this experiment.

In summary, the species interactions in this community appear to be asymmetric, with the response of a species to competition and the competitive effect of the species on others being negatively correlated. This creates a hierarchy of species' competitive ability and this hierarchy, along with a lack of specificity of interactions, suggests that all the species in this community are limited by and competing for the same resource or resources. The hierarchy of competitive ability appears in large part to determine the abundance of each species in the full community.

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