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THE RESPONSE OF ANNUALS IN COMPETITIVE NEIGHBORHOODS: EFFECTS OF ELEVATED CO₂¹

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Abstract. Four members of an annual community were used to investigate the effects of changing neighborhood complexity and increased CO₂ concentration on competitive outcome. Plants were grown in monoculture and in all possible combinations of two, three, and four species in CO₂-controlled growth chambers at CO₂ concentrations of 350, 500, and 700 μ L/L with ample moisture and high light.

Species responded differently to enhanced CO₂ level. Some species (e.g., *Abutilon theophrasti*) had increased biomass with increasing CO₂, while others (e.g., *Amaranthus retroflexus*) had decreased biomass with increasing CO₂ concentration. In mixtures, species tended to interact strongly, and, in some cases, the interaction canceled out the effects of CO₂. Furthermore, there were clear differences in species behavior in different competitive mixtures as assessed by total biomass and seed biomass, and by an index of response to neighbors. In general, competitive arrays that had C₃ species depressed the response of C₄ species, especially *Amaranthus*. *Ambrosia artemisiifolia* was the strongest competitor in this assemblage. Strong statistical interactions between CO₂ and the identity of the competing species in mixtures were found to be primarily due to the as yet unexplained response of plants with CO₂ at 500 μ L/L. The potential effects of CO₂ on community structure could be profound, particularly at the intermediate levels of CO₂ that are predicted to be reached during the first half of the next century.

Key words: *Abutilon theophrasti*; *Amaranthus retroflexus*; *Ambrosia artemisiifolia*; *annuals*; CO₂; *competition*; *equivalence*; *Setaria faberii*.

INTRODUCTION

Increasing atmospheric CO₂ is generally predicted to lead to higher productivity in plants grown as individuals. This has been shown to hold true for a number of plant species (review in Strain 1985). However, in communities, while overall productivity usually increases, specific species response may be quite unpredictable (review in Bazzaz et al. 1985a, Tissue and Oechel 1987). In a six-species mixture Zangerl and Bazzaz (1984) found that vegetative biomass increased with increasing CO₂ in two species (both C₃) but was unchanged in four other species (two C₃ and two C₄). Reproductive biomass increased in four of the species (two C₃ and two C₄) and was unchanged in one other (C₃). The sixth species (*Chenopodium album*) failed to reproduce during the experiment.

Several studies have shown that the relation between plant growth and CO₂ concentration is not always linear and sometimes not even significant (e.g., Garbutt and Bazzaz 1984, Cure 1985, Sionit et al. 1985). This occurs most frequently when plants are grown in competitive arrays. These nonlinear responses may be exaggerated to the point where the response at the intermediate CO₂ level is either much lower or much higher than the response at both the ambient and high CO₂ levels (Zangerl and Bazzaz 1984). Such nonlinear responses in communities complicate the predictions

about change in community composition with increasing CO₂. Since the biotic composition of a neighborhood may have a profound effect on an individual's performance, neighborhood composition is potentially a powerful selective and evolutionary force. Similarly, if the same biotic neighborhood is subjected to different environmental circumstances the interactions among the neighbors may change appreciably (review in Bazzaz 1987). Thus, while there may be no direct effects of an environmental variable on a given target individual, the indirect effects due to the responses of its neighbors may be considerable.

It is convenient to consider the effects of one species on a target species in terms of the change in some measure of productivity relative to the level of productivity in a monoculture of the target species. Interactions may be positive, neutral, or negative. A positive interaction may arise simply by a lessening of intra-specific competition. If two or more species affect the response of the target species to the same degree, we consider these species to be competitively equivalent (*sensu* Parrish and Bazzaz 1982) regardless of the nature of the interaction.

In this study we used four species from an annual community (*Ambrosia artemisiifolia* L., *Abutilon theophrasti* Medic., *Amaranthus retroflexus* L., and *Setaria faberii* Herm.) to investigate the effects of increased CO₂ concentration and changing neighborhood complexity on performance of individuals and competitive outcome. The responses of members of this community are similar on broad resource axes (Bazzaz 1987)

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Planting Designs

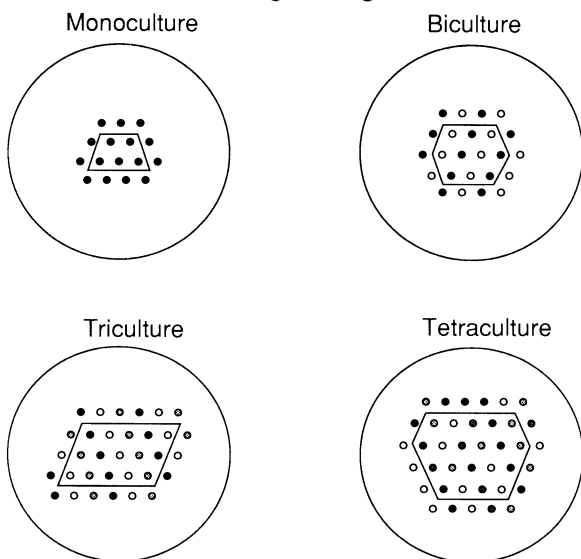


FIG. 1. Planting arrays in the pots: target individuals in each pot are within the polygon, five per species, surrounded by a mixture of border individuals. Density was ≈ 3000 plants/ m^2 . Local density was kept constant, and neighborhood complexity was maximized at each CO_2 level.

and as such might be expected to be competitively equivalent.

METHODS

Seeds of *Ambrosia artemisiifolia* (C_3), *Abutilon theophrasti* (C_3), *Amaranthus retroflexus* (C_4), and *Setaria faberii* (C_4) were collected in September 1984 from an experimental old field near Urbana, Illinois. They were cleaned, stratified in cheesecloth bags, buried in flats of sand, and placed out of doors over winter. The seeds were brought inside in the spring and stored at $4^\circ C$ until needed for the experiment. On 27 August the seeds were planted in sand-filled flats and placed in 12 specially designed growth chambers with CO_2 levels controlled at 350, 500, and $700 \mu L/L$ (detailed description in Bazzaz et al. 1985b). Day temperature was 25° and night temperature 23° . Day length, provided by natural light and supplemented with mercury vapor lamps, was set at 16 h. The photon flux density of photosynthetically active radiation (PAR) was $\approx 2000 \mu mol \cdot m^{-2} \cdot s^{-1}$ on clear days and no less than $900 \mu mol \cdot m^{-2} \cdot s^{-1}$ on cloudy days. On 18 September, the seedlings were transplanted as competitive arrays in 13 cm diameter plastic pots containing a 3:1:1 mixture of sterilized soil, sand, and perlite. These pots were placed in the CO_2 chambers, and the day temperature was raised to 28° .

Each CO_2 chamber contained one pot of each monoculture, all possible two-species arrays, all possible three-species arrays, and the four-species array, totaling 15 pots per chamber. An array consisted of five

target individuals of a species surrounded by a mixture of plants of the competing species (Fig. 1). The arrays were designed to keep local density constant at 3000 individuals/ m^2 and to maximize interspecific neighbor relationships. This design confounded two other factors: (1) decreasing density of any given neighbor with increasing neighborhood complexity, and, because pots were used, (2) increasing global density with increasing complexity of neighborhood.

In order to minimize the effects of changing global density, nutrient supplements were applied three times a week on a per-plant rather than a per-pot basis. Each plant received 0.04 g (in solution) of a standard 12-31-14 NPK nutrient mixture. To test for the effect of global density, 12 pots of each global density (48 pots in all) were planted with a monoculture of *Amaranthus retroflexus* and another 12 at each density were planted with a monoculture of *Ambrosia artemisiifolia* and placed in the chambers. Watering was provided by an automatic drip feed system three times daily. Thirty-five days after transplanting, day length was reduced to 12 h to induce flowering, and individuals of all species had flowered by day 48. Plants were harvested on day 72. They were dried, and then total aboveground biomass and total seed biomass were weighed for each plant.

Statistical analysis

The experiment was a split-plot design for purposes of analysis of variance. Pot means were calculated for each species and used in the analysis to prevent pseudoreplication. Transforming the data did not significantly improve homogeneity of variances, but since the models used are robust to nonhomogeneity of variances (Scheffé 1959: Chapter 10) untransformed data were used in the analysis. Analysis was carried out using the GLIM package (Payne 1985) on an IBM-PC XT.

Response to neighbors (ρ_{ij}) was calculated as

$$\rho_{ij} = (Y_{ij} - \bar{Y}_{ii}) / \bar{Y}_{ji},$$

where Y_{ij} is the productivity of an individual of species i in the presence of species j , \bar{Y}_{ii} is the mean productivity of species i in monoculture, and \bar{Y}_{ji} is the mean productivity of the j^{th} species when grown with species i . This model assumes additivity of response. When there were more than two species in a mixture, \bar{Y}_{ji} was calculated as the mean productivity of all the neighbors in the presence of species i in that particular mixture. Untransformed data were used to calculate response (ρ_{ij}) (Trenbath 1976). Multiple differences were calculated using the Student-Newman-Keuls test.

To establish competitive hierarchy, aggressivity (γ_{ij}) (after Jacquard 1970 and Trenbath 1976) was calculated as

$$\gamma_{ij} = 1/2(Y_{ij} - \bar{Y}_{ii}) + 1/2(Y_{ji} - \bar{Y}_{jj}),$$

where Y_{ij} , etc., are as above. This model also assumes

TABLE 1. ANOVA table for total biomass and total seed mass. Factors are CO₂ concentration, species, and mixture of competing species nested within species (mixture[species]).

Sources	Total community biomass (g)			
	SS	df	MS	F
Block	3.54	3	1.18	1.19 NS
CO ₂ concentration	4.34	2	2.17	2.19 NS
Error (1)	5.97	6	0.99	
Species	989.20	3	329.73	255.39***
Mixture(species)	406.80	28	14.53	11.25***
CO ₂ × species	55.72	6	9.29	7.19***
CO ₂ × mixture(species)	98.28	56	1.76	1.36*
Error (2)	358.92	278	1.29	
Total	1922.20	382		

Sources	Total community seed mass (g)			
	SS	df	MS	F
Block	1.04	3	0.35	26.46***
CO ₂ concentration	0.09	2	0.04	3.29 NS
Error (1)	0.08	6	0.01	
Species	16.47	3	5.49	188.42***
Mixture(species)	7.10	28	0.25	8.70***
CO ₂ × species	1.42	6	0.24	8.12***
CO ₂ × mixture(species)	2.87	56	0.05	1.76***
Error (2)	8.10	278	0.03	
Total	37.16	382		

* $P < .5$; *** $P < .001$.

additivity of response. Significance of differences in γ_{ij} were determined using a nonparametric Student-Newman-Keuls test (Zar 1984).

RESULTS

Analysis of the monoculture of *Amaranthus retroflexus* and *Ambrosia artemisiifolia* grown at different global densities showed no significant effect ($.1 < P < .5$), indicating, at least for these species, that global density effects were not confounded with competitive array effects.

There was a significant effect of species ($P < .001$) on both biomass and seed production. This was the largest effect detected (Tables 1 and 2). There was no significant effect of CO₂ on the overall community biomass or on community seed production (Tables 1 and 2). There were, however, significant CO₂ × species interaction effects for both characters, indicating that the response to CO₂ is species specific.

A. artemisiifolia showed a significant increase in biomass production ($P < .05$) at CO₂ levels of both 500 and 700 $\mu\text{L/L}$ (Fig. 2a). Seed production in this species increased significantly with CO₂ at 500 $\mu\text{L/L}$ ($P < .05$), but was not significantly greater at 700 $\mu\text{L/L}$ than at 350 $\mu\text{L/L}$ CO₂ (Fig. 2b). There was also a significant CO₂ × competitive array interaction in seed production ($P < .01$), which was due primarily to increased productivity of *A. artemisiifolia* in mixtures containing *Amaranthus retroflexus* with a CO₂ concentration of 500 $\mu\text{L/L}$.

There was a marginally significant response to CO₂ ($.05 < P < .1$) in biomass production in *Abutilon theophrasti*, due to a decline in biomass at a CO₂ level of

500 $\mu\text{L/L}$ rather than an increase at 700 $\mu\text{L/L}$ (Fig. 2c). There was, however, a significant increase in seed production ($P < .05$) at 700 $\mu\text{L/L}$ (Fig. 2d). There were no significant interactions between CO₂ and competitive array for the response of *A. theophrasti*.

Amaranthus retroflexus (C₄) showed a significant response to CO₂ in both biomass ($P < .05$; Fig. 2e) and seed production ($P < .01$; Fig. 2f). These responses were entirely attributable to a massive decline in productivity at a CO₂ concentration of 500 $\mu\text{L/L}$, which occurred for this species in all treatments. *Setaria faberii*, also C₄, showed no significant response to CO₂, as might be expected from a C₄ species (Fig. 2g and h). There were no CO₂ × competitive array interactions in the response of *Setaria faberii*.

Response in different neighborhoods

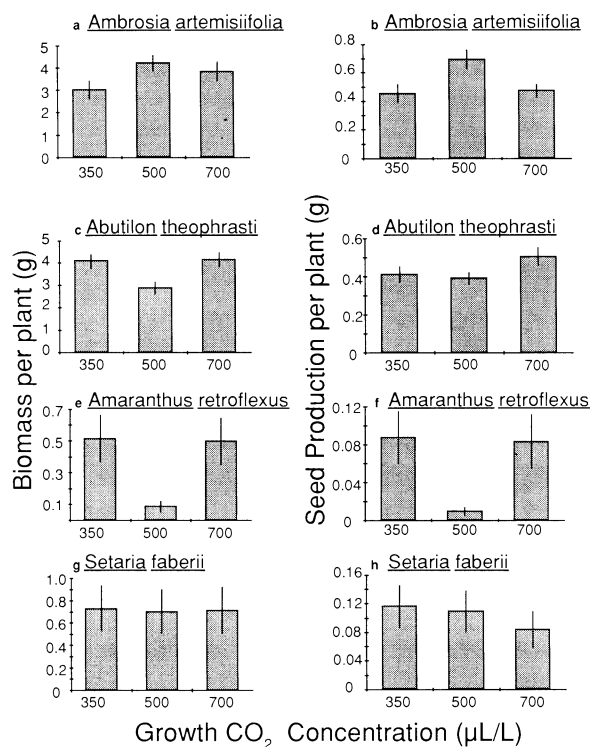
The effect of competition may be considered in two ways. First, in terms of increasing complexity of neighborhood, is there an effect due simply to the number of species involved in a competitive interaction? Second, in terms of the particular identity of the species in the arrays, does it matter what the identities of the competitors are?

Although there was no significant overall response the four species did react differently to the number of species in an array. There was a significant interaction between target species and number of competing species, indicating that response to complexity of competitive array was species specific. While *Ambrosia artemisiifolia* and *Abutilon theophrasti* were not affected by increasing complexity of competitive array in either biomass or seed production, both *Setaria faberii* and

TABLE 2. ANOVA table for total biomass and total seed mass. Factors are CO₂ concentration, species, and number of competitors (complexity of competition).

Source	Total community biomass (g)			
	ss	df	MS	F
Block	3.54	3	1.18	1.19 NS
CO ₂ concentration	4.34	2	2.17	2.18 NS
Error (1)	5.97	6	0.99	
Species	989.20	3	329.73	152.28***
Number of competitors	2.59	3	0.86	0.40 NS
Species × number	123.30	9	13.70	6.33***
Species × CO ₂	55.95	6	9.33	4.31***
Number × CO ₂	1.37	6	0.23	0.11 NS
Species × number × CO ₂	30.59	18	1.70	0.79 NS
Error (2)	705.88	326	2.17	
Total	1922.70	382		

Source	Total community seed mass (g)			
	ss	df	MS	F
Block	1.04	3	0.35	26.46***
CO ₂ concentration	0.09	2	0.04	3.29 NS
Error (1)	0.08	6	0.01	
Species	16.47	3	5.49	117.49***
Number of competitors	0.20	3	0.07	1.39 NS
Species × number	1.77	9	0.20	3.57***
Species × CO ₂	1.44	6	0.24	5.14***
Number × CO ₂	0.31	6	0.05	1.11 NS
Species × number × CO ₂	0.54	18	0.03	0.64 NS
Error (2)	15.23	326	0.05	
Total	37.16	382		

*** $P < .001$.FIG. 2. Mean biomass production and mean total seed mass at each CO₂ level. Bars indicate ± 2 SE.

Amaranthus retroflexus were sensitive to increasing complexity for biomass ($P < .001$ for both species) and seed production ($P < .01$ for *A. retroflexus*, $P < .001$ for *S. faberii*). In both species, productivity was highest either in monoculture or in two-species array with the other C₄ species (Figs. 3 and 4). *A. retroflexus* was the only species that showed a significant number \times CO₂ interaction ($P < .05$ for seed production). This was due once again to the reduced productivity of *A. retroflexus* at a CO₂ level of 500 µL/L.

The response to specific species combination type (or mixture) was nested within species for the purposes of analysis of variance. This term, mixture within species, was found to be significant overall for both biomass and seed production (both $P < .001$; Table 1).

The only case in which the effect of mixture was not significant was seed production in *Abutilon theophrasti*, which was remarkably uniform over all mixtures (Fig. 4). All the other species showed clearly different responses dependent on the composition of the mixture (Figs. 3 and 4).

Analysis of response to neighbors (ρ_{ij})

Overall response to neighbors (ρ_{ij}) was not affected by CO₂ (Table 3). In fact, for seed production, there were no significant terms involving CO₂. Response to neighbors based on biomass did show significant CO₂ interaction terms (Table 3); these were found to be due

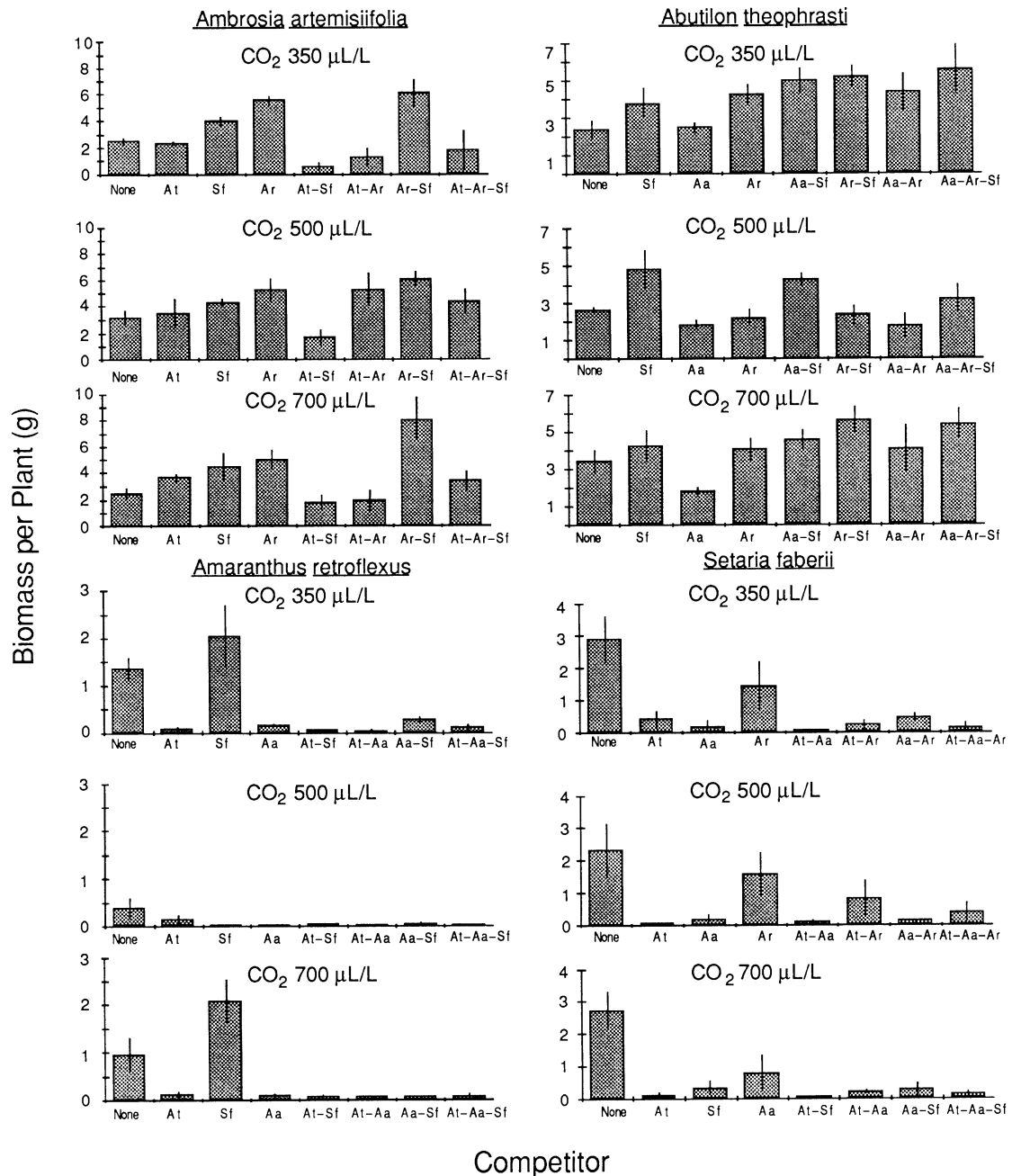


FIG. 3. Mean biomass production per plant at each CO₂ level and in each species mixture (At = *Abutilon*, Aa = *Ambrosia*, Ar = *Amaranthus*, Sf = *Setaria*). Bars indicate ± 2 SE.

entirely to the effects of mixtures grown at 500 $\mu\text{L/L}$, particularly those containing *Amaranthus retroflexus*. Because there were no significant differences in response between CO₂ concentrations of 350 $\mu\text{L/L}$ and 700 $\mu\text{L/L}$, the data from 500 $\mu\text{L/L}$ were dropped, and the remaining data were pooled for analysis of equivalence of neighbors.

The general patterns of response were similar for both biomass and seed production (Fig. 5). Any mixture containing *Abutilon theophrasti* had an approxi-

mately equivalent effect on the response of *Ambrosia artemisiifolia*, which was also very similar to the effect of monospecific competition. The response of *A. artemisiifolia* in mixtures containing C₄ species, but not *Abutilon theophrasti*, was quite different from those containing *A. theophrasti*. In those mixtures without *A. theophrasti* response of *A. artemisiifolia* was enhanced over that in monoculture (Fig. 5a and b). The response of *A. theophrasti* with regard to equivalence of biomass was similar to that of *A. artemisiifolia*, ex-

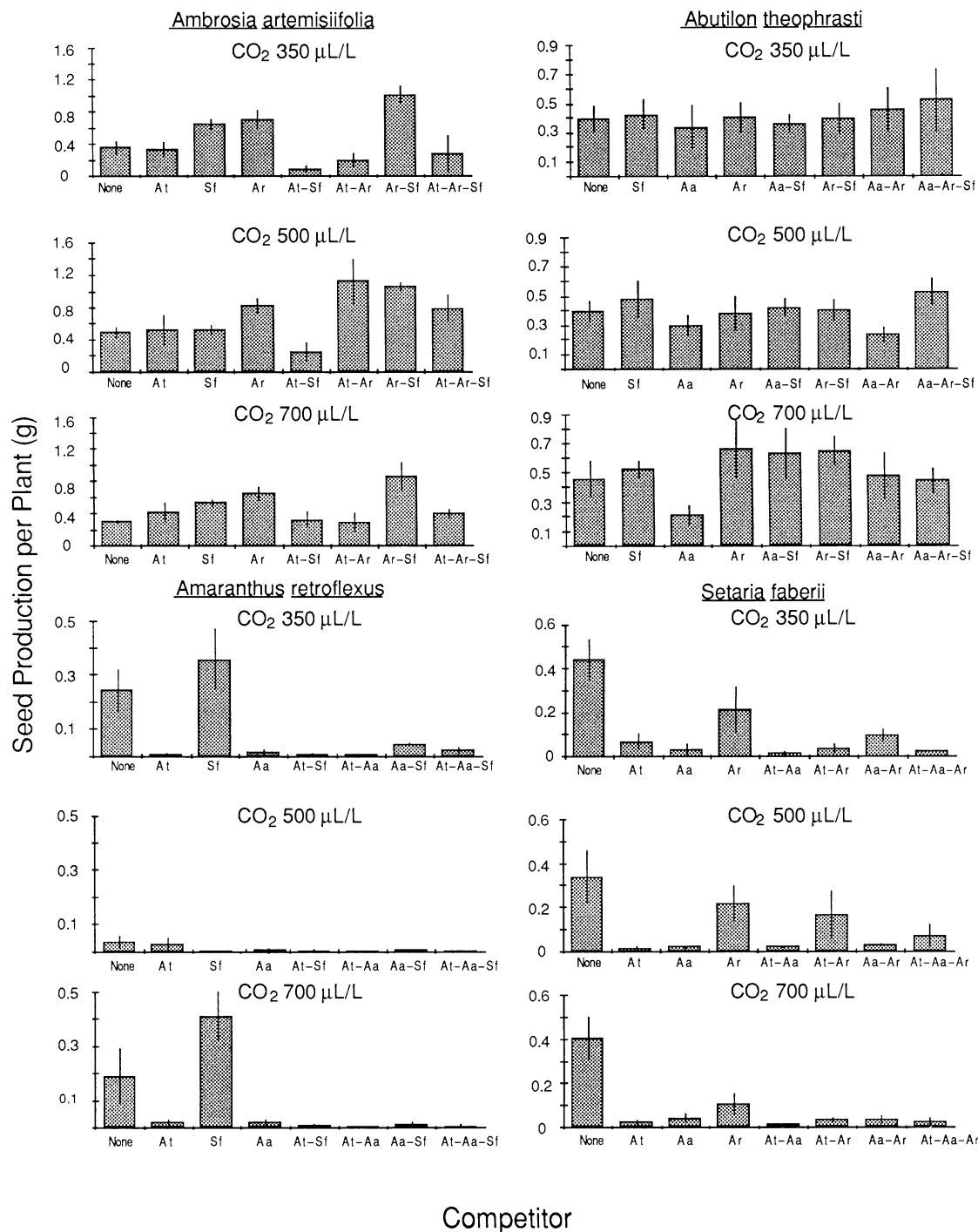


FIG. 4. Mean total seed mass per plant at each CO₂ level and in each species mixture (At = *Abutilon*, Aa = *Ambrosia*, Ar = *Amaranthus*, Sf = *Setaria*). Bars indicate ± 2 SE.

cept that the C₃–C₄ dichotomy was not as clear. In *A. theophrasti* the response of seed production to neighbors showed very large variations, and while the pattern was similar to that observed for biomass, the responses were not judged significantly different (Fig. 5e and f). All mixtures containing C₃ species proved to

be deleterious, relative to monoculture, in *A. retroflexus* for both seed production and biomass. These responses were not judged to be significantly different from each other and therefore may be equivalent. Growth with *Setaria faberii* enhanced the response of *A. retroflexus* (Fig. 5e and f). All mixtures had a neg-

ative effect on *S. faberii*. No clear patterns emerged, however, only a tendency for mixtures containing more than two species to be less deleterious than two-species arrays (Fig. 5g and h).

A. artemisiifolia was clearly the most aggressive species followed by *A. theophrasti*, *A. retroflexus*, and finally *S. faberii* (Table 4).

DISCUSSION

Response to elevated CO₂

The results of this study were unusual in that overall productivity in neither biomass nor seed production increased significantly with increased CO₂ concentration. In previous studies, using members of the same community, increased productivity has been found at the community level even in those instances where some species failed to respond to increased CO₂ (Bazzaz et al. 1985a). Zangerl and Bazzaz (1984) investigated the response of six species, including the four in this study, to CO₂ and different levels of nutrients and light. In low nutrients and low light, there was little increase in biomass. In most of the other environments there was an increase in community productivity, which was mainly caused by the increase in one particular species, *Polygonum pensylvanicum*. Since this species was not included in the present study the extremely varied responses shown by the other species must be a reflection of their specific response to elevated CO₂.

If we consider the response of the species at a CO₂ level of 700 μ L/L relative to that at 350 μ L/L we would predict that, while there would be no increase in community total seed production, there would be a change in species composition. *Abutilon theophrasti* would be expected to increase in the community, while *Setaria faberii* should decrease. Comparing the response at 500 μ L/L with that at 350 μ L/L we would predict that *Abutilon theophrasti* should remain constant as should *Setaria faberii*. *Ambrosia artemisiifolia* would be predicted to increase, and *Amaranthus retroflexus* to decrease, substantially.

It has not been customary to investigate the responses of plants to intermediate levels of CO₂. Kimball (1983) reported 770 observations of the effects of increasing CO₂ on yield, mainly in agricultural species. Of these observations only 121 used more than two levels of CO₂, and of these 121, 26 had yields at intermediate CO₂ levels that were either greater than or less than those at both the high and low CO₂ levels. In most other cases the intermediate response was indistinguishable from one of the other treatments.

Zangerl and Bazzaz (1984) showed that the response observed at 450 μ L/L relative to that at 350 μ L/L and that at 600 μ L/L was highly influenced by the number of species and conditions. For example, under conditions of high nutrient availability, *A. artemisiifolia* produced more seed at CO₂ at 450 μ L/L than at both 350 μ L/L and 600 μ L/L. Similarly in the present study (Fig. 2b) *A. artemisiifolia* showed in-

TABLE 3. ANOVA table for total biomass and total seed mass based on \bar{A}_{ij} values for response to neighbors. Factors are CO₂ concentration, species, and mixture of competing species nested within species (mixture[species]).

Sources	Total community biomass (g)			
	ss	df	ms	F
Block	5.33	3	1.78	0.003 NS
CO ₂ concentration	348.30	2	174.15	3.08 NS
Error (1)	339.70	6	56.62	
Species	2445.00	3	815.50	61.29***
Mix(species)	5916.00	24	246.50	18.54***
CO ₂ \times species	451.10	6	75.18	5.65***
CO ₂ \times mix(spec)	4770.00	48	99.38	7.47***
Error (2)	3138.80	236	13.29	
Total	17415	328		
Sources	Total community seed mass (g)			
	ss	df	ms	F
Block	271.00	3	72.33	8.77*
CO ₂ concentration	30.61	2	15.31	1.86 NS
Error (1)	49.47	6	8.25	
Species	1723.00	3	574.33	28.03***
Mix(species)	4717.00	24	196.54	9.59***
CO ₂ \times species	109.90	6	18.32	0.89 NS
CO ₂ \times mix(spec)	858.10	48	17.88	0.87 NS
Error (2)	4835.80	236	20.49	
Total	12595	327		

* $P < .5$; *** $P < .001$.

creased seed production at 500 μ L/L. However, at intermediate nutrient levels Zangerl and Bazzaz (1984) found that *A. artemisiifolia* produced less seed than at either 350 μ L/L or 600 μ L/L. These authors also found that biomass production was moderately depressed at intermediate CO₂ in *A. retroflexus* but did not find a similar response in seed production. The depression in both biomass and seed production found in the present study (Fig. 2) for this species was much more pronounced.

Our study and those cited above show that response at intermediate CO₂ levels (400–500 μ L/L) is both species and environment specific. We also found that competitive interactions were modified more at 500 μ L/L than at 700 μ L/L. In fact, most of the CO₂ \times competition term, whether as number of competitors, specific type of competitor, or based on equivalence of competitors, could be explained by changing interaction with CO₂ at 500 μ L/L rather than 700 μ L/L. If these observations about the large "intermediate effect" are truly representative, and given the expected slow rise in global CO₂ concentrations relative to the generation time of the annuals, the community compositions we observed at 700 μ L/L may never come into existence in nature, as the material necessary for them may be substantially altered through selection via differential success at intermediate CO₂ levels. In order to understand the true impact of increasing CO₂ levels it will be necessary to set up experiments that monitor productivity over a number of generations with CO₂ being raised gradually at each generation.

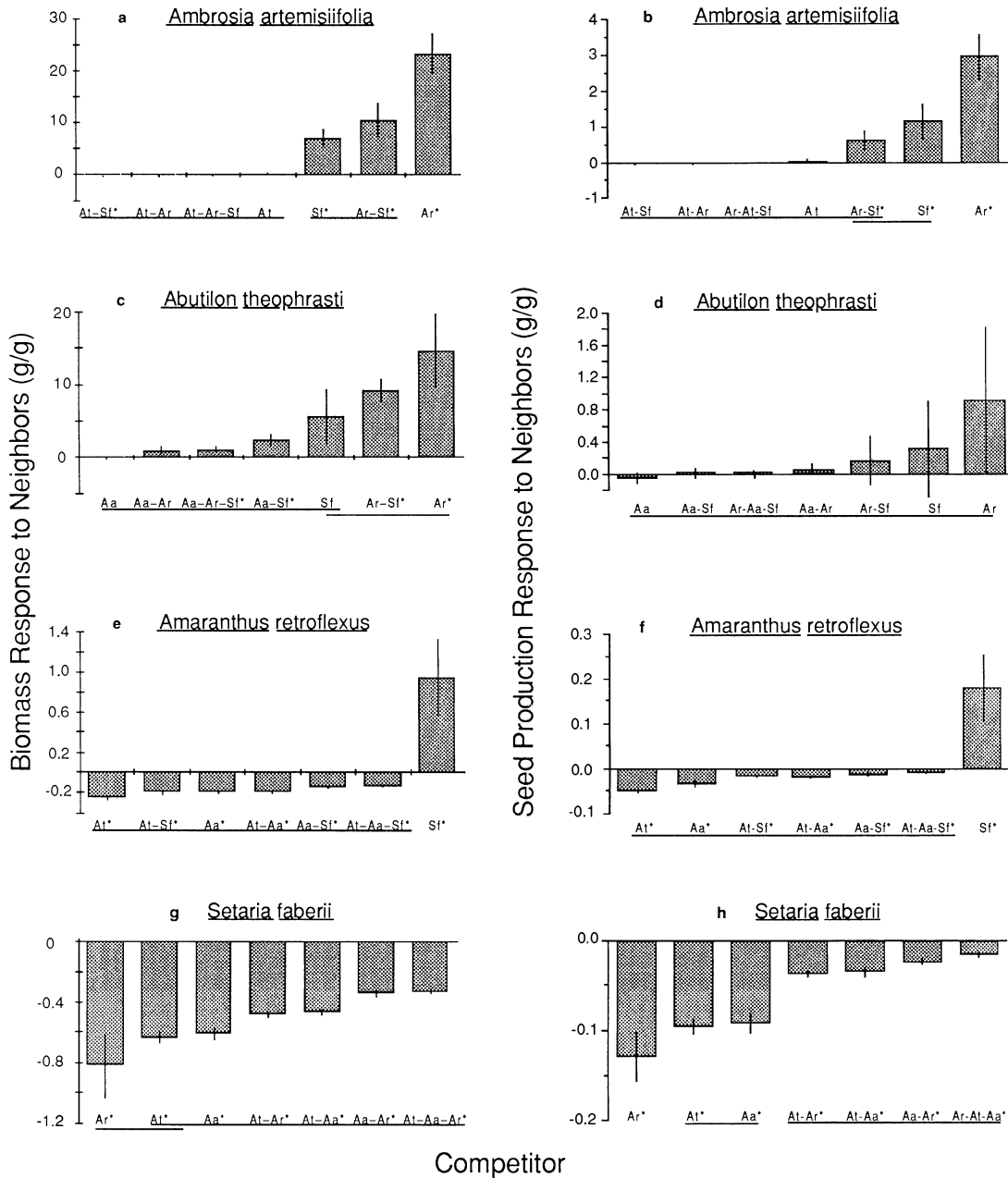


FIG. 5. Mean biomass difference (in grams) between a species' productivity in mixture and in monoculture per biomass of competitor(s) (in grams) and mean seed mass difference (in grams) per biomass competitor(s) (in grams) for each competitive array (At = *Abutilon*, Aa = *Ambrosia*, Ar = *Amaranthus*, Sf = *Setaria*). Codes on the same line were not significantly different from each other by a Student-Newman-Keuls test. * Significantly different from zero.

Species interaction and equivalence of neighbors

Our previous work with these species' performance on resource gradients suggested a high level of equivalency of neighbors. The coefficient of variation of the ratio of mean individual biomass in monospecific stands for all species was quite low in this community. That is, differences in performance among species were small, suggesting that they are more or less equivalent as tar-

gets (Parrish and Bazzaz 1982, Goldberg and Werner 1983). The apparent sensitivity of *Amaranthus retroflexus* and *Setaria faberii* to increasing complexity of neighborhood (Figs. 3 and 4) may be because all neighborhoods of three or more species would contain at least one C_3 species. In both of these C_4 species biomass and seed production were reduced in the presence of C_3 species more than in the presence of another C_4 species. All species showed differential performance

TABLE 4. Aggressivity (γ_{ij}) for each species. Values with the same letter in any given row are not significantly different based on nonparametric Student-Newman-Keuls test.

Target	Competitor biomass				Mean
	<i>Abutilon</i>	<i>Amaranthus</i>	<i>Ambrosia</i>	<i>Setaria</i>	
<i>Abutilon</i>	0.00 A	0.56 B	-0.21 C	0.75 B	0.275
<i>Amaranthus</i>	-0.56 A	0.00 B	-0.93 A	0.41 B	-0.270
<i>Ambrosia</i>	0.21 A	0.93 B	0.00 A	0.75 B	0.473
<i>Setaria</i>	-0.75 A	-0.37 AB	0.75 A	0.00 B	-0.468
Target	Competitor seed production				Mean
	<i>Abutilon</i>	<i>Amaranthus</i>	<i>Ambrosia</i>	<i>Setaria</i>	
<i>Abutilon</i>	0.00 A	0.43 B	-0.21 A	0.53 B	0.188
<i>Amaranthus</i>	-0.43 A	0.00 B	-0.92 C	0.41 B	-0.235
<i>Ambrosia</i>	0.21 A	0.92 B	0.00 A	0.73 B	0.465
<i>Setaria</i>	-0.53 A	-0.37 AB	-0.73 A	0.00 B	-0.408

among neighborhood types. This, however, does not necessarily indicate that there was no equivalence of response, as the measure of response to neighbors is made up of two components. The first is the difference between productivity of a species in a mixture and in a monoculture ($Y_{ij} - \bar{Y}_{ji}$) (Figs. 3 and 4). The second is the mean productivity of neighbors (\bar{Y}_{ji}) in the mixture, and this will also vary from mixture to mixture. Thus, equivalence is estimated as the difference between a species' mass in mixture and in monoculture per mass of the neighbor productivity; hence differences of 2 and 8g would be judged equivalent if the neighbor productivity were 1 and 4g, respectively. It should be noted that the parameter (\bar{Y}_{ji}) need not be in the same units as the numerator; it can be any measure of individual or species performance. In studies where plant number has not been controlled the number of neighbors of a particular species might be an appropriate standardization. In this experiment, as number was invariate, biomass was more appropriate.

While we can use ANOVA to determine which neighborhoods do not produce equivalent responses, it is difficult, without committing type II error, to determine which neighborhoods do produce equivalent responses.

Because of the low power of the multiple comparison test, only a few definitive statements may be made about equivalence. Any combination of species containing a C_3 species had a negative effect on *Amaranthus retroflexus*, and these combinations are more or less equivalent. *Setaria faberii* showed negative responses in all mixtures, and again it may be that the effects of a mixture containing a C_3 species are equivalent. Patterns shown by *Abutilon theophrasti* and *Ambrosia artemisiifolia* were similar. Combinations containing C_3 species were, on the whole, neutral and more or less equivalent, while combinations containing C_4 species had a positive effect in terms of difference between mass in mixture and in monoculture per mass neighbor productivity.

In this community there were species-specific responses to CO_2 . These were both negative and positive, canceling out the effects of CO_2 on productivity at the

community level. The potential effects of CO_2 on community structure could be profound, particularly as the response to intermediate levels of CO_2 (400–500 $\mu L/L$) is extremely varied and leads to different predictions about the future community structure than does the response at a CO_2 concentration of 700 $\mu L/L$.

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