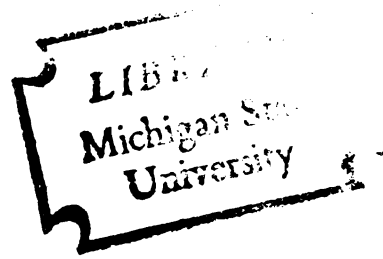


THE EFFECTS OF PATTERN ON THE RELATIVE
YIELDS OF FOUR FIRST YEAR
FALLOW FIELD SPECIES

A Dissertation
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Glenn Clinton Kroh
1975



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ABSTRACT

THE EFFECTS OF PATTERN ON THE RELATIVE YIELDS OF FOUR FIRST YEAR FALLOW FIELD SPECIES

By

Glenn Clinton Kroh

Two hypotheses were tested: first, that a diverse array of plants will out-yield a less diverse array of plants, on the same site with plant density fixed, and second, that when the pattern of positions of individuals of different species, in an array with fixed density and diversity, is changed, overall yield may be altered as a result of change in competitive stress among individual plants. The four species used were Amaranthus retroflexus, Chenopodium album, Panicum capillare, and Setaria viridis. Mixtures containing four species each and pure stands of each species were grown. The mixture plots had fixed distributions of species in equal proportions but in different patterns. Interplant distance was 15 cm, giving an effective density of 51 plants/m². At the end of the growing season, the plants were harvested, dried and weighed. Pure stands of Amaranthus produced higher yields than any of the mixtures. Yields among mixture plots with different patterns did not differ significantly. A second study was run concurrently with the above study to determine the feasibility of using results of a paired-species competitive ability experiment as a

Glenn Clinton Kroh

predictor of the outcome of different combinations of species. The five treatments consisted of competition from each of the four species plus a control. Each treatment was composed of a "target" plant surrounded by six competitor plants. Controls were single plants without competitors. The outcome of different combinations could not be predicted from the results of this experiment. Below ground biomass was sampled and estimations of root yields were lower than expected. However, data collected indicated that dicot roots suppress root growth of neighboring plants more than the monocots.

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OF FOUR FIRST YEAR FALLOW FIELD SPECIES

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Glenn Clinton Kroh

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INTRODUCTION

Diversity Versus Net Primary Productivity (NPP)

One of the most important parameters of a community is the net primary productivity (NPP) (Woodwell and Whittaker, 1968). This is the amount of biomass produced by the plant component of the community, which will be the energy source for the heterotrophic organisms.

Robert McIntosh (1970) commented, "The conventional wisdom of ecologists is that diversified utilization of site resources should result in greater productivity and efficiency." In other words, niche specialization would not only allow more species to coexist in an area, but also enable them to physiologically and morphologically exploit a resource base more thoroughly. Depending on the type of community present, one could judge its success at utilizing the resources of a particular site by resultant productivity, yield, viability of seeds, or persistence of the community through time. As yet, only one study (Werner, 1972) has indicated that increase in species number in a particular plant array increases the productivity or yield of a particular site.

In an ecological sense, diversity of a community relates to the richness and evenness of species within that system. Richness refers to the number of species or functional groups while evenness is a measure of the relative proportions of those species or groups

within the community. Evidence strongly supports the hypothesis that diversity is inversely related to NPP within a given community (Margalef, 1963; McNaughton, 1967, 1968; Stephenson, 1973). When site potential is increased, planktonic communities respond with increased NPP and decreased diversity (Margalef, 1963; Patrick, 1949). McNaughton (1968) demonstrated that the most productive sites in annual California grasslands have lower diversities than less productive sites. In a study on the community dynamics of a mid-Michigan oldfield, Stephenson (1973) utilized NPP as an experimental variable by enhancing site potential through enrichment of the soil with fertilizer treatments. The most productive arrays of plants exhibited the lowest diversities.

Mixture-Yield Studies

One approach to studying the relationship of diversity to productivity in plant arrays is to conduct mixture-yield experiments. Literally hundreds of pair-wise competitive ability experiments have been completed with plant populations (see reviews by Donald, 1963; Harper, 1961; McIntosh, 1970). Watt (1964) suggested it was possible to rank a group of plants by their respective competitive abilities and consequently predict the outcome of different combinations. Paired-species experiments have shown that mixture yields fall in between those of the highest and lowest yielding pure stands of the component species (Donald, 1963). A clear exception to these results was demonstrated by Whittington and O'Brien (1968). They stated that failure of other studies to demonstrate mixtures that were higher yielding than pure stands of the component species was probably due

(1) to use of species that were not suppressed a great deal by intra-specific competition, (2) use of species not differing significantly in their patterns of root growth, (3) use of shallow pots or boxes that restricted root growth and finally (4) use of species in which one or both were suppressed greatly through interspecific competition. Their study explored the competitive interactions of rye grass, meadow fescue and a triploid of rye grass. Under certain clipping treatments, mixtures yielded more biomass than pure stands.

Plant mixture studies involving more than two species have shown that mixtures do not out-yield pure stands of the most productive species in the mixtures. Bornkhamm (1961) ran a mixture study using white mustard (Sinapsis alba), corn cockle (Agrostema githago), cheatgrass (Bromus secalinas) and pimpernel (Anagallis arvensis). He grew these species in pots as pure stands, two-species mixtures, three-species mixtures and four-species mixtures. All mixtures were equi-proportionate, with regard to the separate species. Pure stands of white mustard out-yielded all of the mixture plots, while pure stands of pimpernel had the lowest yield in the experiment. Another diversity-yield experiment (Haizel, 1972), using three species, had similar results to those of Bornkhamm (1961). Haizel planted barley (Hordeum vulgare), white mustard (Sinapsis alba) and poppy (Papaver rhoeas) in pure stands, two-species mixtures and three-species mixtures. He repeated the experiment, using wild oats (Avena fatua) in place of poppy. In his summary of the experiment, he says "On no occasion did the yield of any of the mixtures exceed the highest yielding species in pure stand." These studies have not demonstrated that NPP increases with diversity.

Crop Mixtures versus Yield

There is very sparse evidence concerning greater yields in mixtures of crops than yields in monoculture (Loomis, 1971; Rhodes, 1970). Loomis feels a synergistic relationship among two species of crops seems unlikely, with regard to use of available light, the principal limiting factor in intensive agriculture. He argues that since a single species can be grown at a sufficient density to completely intercept available light, the resource benefit cannot be increased by establishing a mixture of plants with "diverse stature and leaf display". It would seem if mixtures of crops did, in fact, commonly out-yield pure stands, that the practice of multiple-crop farming would be in frequent use today.

In regions where hand implements are used at sowing and harvest, man has developed mixed cropping (Donald, 1963). Examples can be found in Ceylon where pastures or bananas are grown beneath coconut palms; in the Mediterranean where wheat is planted among olive plants or cork oaks and in Greece where alternate rows of cotton and corn are sown, under irrigation. There does not seem to be data available concerning yields of these mixtures versus those of the component species in pure stands.

Pattern versus Yield

Altering the arrangement (pattern) of individuals within a given plant array may affect the NPP and resultant yield of that array. When studying the inter-varietal competitive abilities of barley and rice, Sakai (1957) developed and used an experimental design incorporating the use of a six-member competitor ring. One plant variety

was individually planted and encircled by (1) six plants of the same variety, (2) five of the same and one of the other, (3) four of the same and two of the other, and so on, until all six plants were of the other variety. He found a linear relationship between the yield of the target (center) plant and the number of plants in the ring of the variety with the best competitive ability. Harper (1961) did an experiment using Bromus rigidus and B. madritensis at equal densities. Five plant patterns of the two species were used. Individual plants were sown into hexagonal patterns that allowed (1) each plant to be surrounded by three of its own species and three of the other, (2) two of its own species and four of the other, (3) four of its own species and two of the other, (4) random placement of each species on the hexagonal pattern and finally (5) a completely random pattern in the pot. Total yield was not significantly affected by changes in the pattern. However, there were definite differences in the proportional contributions made by the two species to the total biomass. Further, contrary to the findings of Sakai (1955), there was not a linear relationship between the suppression of growth of B. madritensis and the number of B. rigidus plants in the surrounding hexagon.

Allocation of Site Resources among Species

In natural plant communities, the allocation of available site resources is rarely equally distributed among the different species populations. Relative success of a species at utilizing the available resources of a particular site can be quantitatively expressed by an importance value (Cox, 1967). Importance value refers to the sum of the relative frequency, relative density, and relative dominance of

a species within a particular array of plants. Whittaker (1969) suggests that if it is assumed that there is some correspondence between the share of the community's resources a species utilizes, the share of the niche space it occupies, and the share of the community's productivity it realizes, then relative importance values can be expressed as relative niche sizes. There are three hypotheses on how niche space is divided to produce the distribution of productivity among species within an array. The random niche boundary hypothesis, as proposed by MacArthur (1957, 1960), states that the boundaries of niches are located at random in niche hyperspace. This type of distribution is found in some animal communities (King, 1964; Hairston, 1964) and in particular with territorial birds (MacArthur, 1960). The second is the log normal hypothesis put forth by Preston (1948, 1962). Basically, it says that species importance values are determined by independent variables and that species importance will then approach a normal frequency distribution for which a logarithmic scale of importance is appropriate. Communities that are rich in species generally exhibit this type of distribution. The niche pre-emption hypothesis (Whittaker, 1965, 1969) states that the most dominant species pre-empt a given fraction of the total niche space. The second most dominant species then takes a similar fraction of the remaining space and the third most dominant species takes a similar fraction of the remaining niche space not utilized by the first two species and so on down to the last species in the community. This distribution seems to be characteristic of communities with low species richness.

Intra- versus Interspecific Competition

In this study, the term competition is used in the manner that Harper (1961) uses the term interference to mean "...those hardships which are caused by the proximity of neighbors..." In this context, "competition" will include both the effects of competition for limited resources and allelopathy among species populations.

All plants utilize light, water, nutrients and carbon dioxide throughout their life cycles. Individual plants within each population have genetic potentials for growth and reproduction. This potential may or may not be realized, depending on the site resources and biological interference from neighboring plants. Plants of the same species tend to utilize, both spatially and physiologically, site resources in the same way. In other words, plants of the same species acquire the same nutrients in the same amounts from the same regions of a particular site. On the other hand, individuals of different species presumably utilize a site in different ways. The term annidation has been used by Ludwig (Ludwig, in Harper, 1967) to describe the evolutionary process of direct selection for some difference in niche occupancy of species within a community.

Since individuals within a species are thought to occupy the same niche, it is thought that intraspecific competition is more severe than interspecific competition. It is thought that this may be one of the most important underlying mechanisms for control of population sizes in a community (McIntosh, 1970). Several studies, run with two species mixtures, have shown that intraspecific competition exerts a disproportionate mortality rate on the population with the highest number of individuals (Population I). Resultant reduction

in size of Population I reduces interspecific competition stress and allows the previously recessive population (Population II) to become the largest in the mixture. When this occurs, Population II now experiences disproportionate mortality from intraspecific competition with a resultant decrease in numbers and a corresponding increase, once again, in the size of Population I. This self-stabilizing process has been shown to occur from year to year in a grass-clover association (Leith, 1960).

Approaches to the Study of Plant Communities

Many investigators feel that studies of communities, as a whole, are essential to understand the inherent dynamics of the system (Waddington, 1961, 1965; Slobodkin, 1962; Orians, 1962). Rather than the "holistic" approach, Lewontin (1968) prefers an analytical approach to get at the mechanisms of a system. Complex interactions are broken down into simpler components that lend themselves more readily to experimentation than does the whole. As most plant communities are difficult, if not impossible to manipulate experimentally, the latter approach to probing complex interactions of a community is the most pragmatic.

Community ecologists generally believe that competition is an important factor in community dynamics (Poore, 1964; Watt, 1964; Major, 1958). Watt (1964) suggested that it was possible to rank a group of plants by their respective competitive abilities and consequently predict the outcome of different combinations. Harper (1967) felt that "ecological combining properties" of species might be examined in all possible combinations of pairs and their yields

compared with that in pure stands. He felt that in this manner, dominance could be detected and bring "... to experimental synecology a refinement and subtlety appropriate for a science which has outgrown its qualitative and descriptive youth." Although the analytic method will not solve all community level questions, it very well could lead to important insights into those problems.

The analytical approach is used to investigate the relationships discussed in the preceding sections. In general, I have studied the effects of intra- and interspecific competition on above and below ground plant yield. More specifically, I investigated:

1. The hypothesis that productivity and resultant yield are positively related to the diversity of a given system.
2. The hypothesis that altering the arrangement (pattern) of individuals, within a given plant array, will affect the NPP of that array.
3. The expression of dominance and resultant allocation of yield among species within a given plant array.
4. The feasibility of using results of a paired-species competitive ability experiment to predict the relative performances of more than two species, when grown together.

MATERIALS AND METHODS

Selection of Experimental Species

An ideal system for investigation of the diversity-yield relationship is the fallow field community. Annual herbs that complete their life cycles in one growing season are dominant plants in this type of community. Since there are no perennial organs, total above and below ground biomass can be determined.

Mid-Michigan first year fallow field communities contain plant components that are easily manipulated. They are "r" selected colonizers that consequently have highly overlapping niches, providing for greater interference (Odum, 1969). Shoots of these plants exhibit a very flexible growth response to interference from neighboring plants. Since the dominant species are herbaceous annuals, all plants are discrete entities that complete their life cycles in one growing season. The use of biennials and perennials, characteristic of later successional stages, was prohibitive, as they are prone to vegetative reproduction through formation of rhizomes and stolons. Since two or more plants can be attached physiologically, perennial plants cannot be considered as discrete entities. It was with this in mind that annual herbs from the first year fallow field community were used.

Diversity-Yield Experiment

Two experiments were designed and implemented. In both experiments, two dicotyledonous plants, Amaranthus retroflexus and Chenopodium

album, as well as two monocotyledonous plants, Panicum capillare and Setaria viridis, were used. They were selected on the basis of their representativeness of typical plant forms in the first year fallow field communities as well as differences in structure and possibly function of above and below ground biomass. Experiment I involved growing plots of mixtures containing four species and pure stands of each species. Yields of the mixture plots and pure stands were compared and analyzed statistically using a randomized block experimental design, replicated three times. In each block, four plots were monocultures and four were mixtures with fixed distributions of species in equal proportions but in different patterns (Figure 1). Each mixture plot originally contained 128 plants in eight rows of sixteen plants each. The number of plants in the patterns changed throughout the experiment due to mortality of plants originally sown, as well as invasion of plants from the natural seed pool.

Interplant distance was 15 cm, giving an effective density of 51 plants/m². This density was determined by observation of natural fallow field communities which subsequently allowed a qualitative decision concerning the interplant distance to be used in this study. Two rows of each of the four species were in each of the mixture plots. Species were arranged to allow interfacing of all possible combinations of the four species. In addition to the three possible spatial arrangements of rows within the mixture plots, a fourth plot, using a randomized pattern was used. Positions of individual plants of each species within this plot were randomly assigned. As all plots had 128 plants each, a single replicate contained 1024 plants.

Figure 1. Four basic patterns of plants in the mixture plots.

S S S S S S S S S S S S S S S S
 P P P P P P P P P P P P P P P P
 S S S S S S S S S S S S S S S S
 P P P P P P P P P P P P P P P P
 A A A A A A A A A A A A A A A A
 C C C C C C C C C C C C C C C C
 A A A A A A A A A A A A A A A A
 C C C C C C C C C C C C C C C C

CHENOPODIUM (C) - AMARANTHUS (A)
 PANICUM (P) - SETARIA (S)

P P P P P P P P P P P P P P P P
 C C C C C C C C C C C C C C C C
 P P P P P P P P P P P P P P P P
 C C C C C C C C C C C C C C C C
 A A A A A A A A A A A A A A A A
 S S S S S S S S S S S S S S S S
 A A A A A A A A A A A A A A A A
 S S S S S S S S S S S S S S S S

SETARIA (S) - AMARANTHUS (A)
 CHENOPODIUM (C) - PANICUM (P)

S S S S S S S S S S S S S S S S
 C C C C C C C C C C C C C C C C
 S S S S S S S S S S S S S S S S
 C C C C C C C C C C C C C C C C
 A A A A A A A A A A A A A A A A
 P P P P P P P P P P P P P P P P
 A A A A A A A A A A A A A A A A
 P P P P P P P P P P P P P P P P

PANICUM (P) - AMARANTHUS (A)
 CHENOPODIUM (C) - SETARIA (S)

S S C P A A C S P A S A P C A C
 C P S P C S S A A S P S S C A
 P S S P A P C A S C A A P A S
 P C S P C A C S P A C P C P P C
 S A C P S A S A P C C S C A P A
 S C S S C C A S P S A A S A S
 P C P P C P C S C C A S P P C P
 P A S A S A C S P C P C A P S A

RANDOM

FIGURE 1

On June 25, 1973, a cultivated field, previously planted in soybean, was plowed, tilled and harrowed, in preparation for the study. Agricultural soils contain enormous seed pools of annual weeds. In order to assure the integrity of the pattern of experimental plants, some method had to be developed to enable distinction of experimental plants from natural plants. Black polyethylene sheets, one meter by two and a half meters in size, were used for templates. Each sheet had a 128 hole pattern in which experiment seeds were sown. The templates were left in place on the soil for five weeks and then removed. Seeds were sown by hand and the plots were watered equally every three days for the first five weeks. Several seeds were sown per template hole to assure adequate germination. After germination, plants were thinned to one per hole. In the event no seeds germinated in a given plot position, seedlings were transplanted from the reservoir plots. In this regard, Chenopodium had only about 25% germination. As a result, reservoir plots were exhausted and seedlings from the natural population, adjacent to the experimental plots, were used.

On September 15, 1973, all plots were harvested, with plants of individual rows put into coded plastic bags and stored at 5°C. Within each row, several plants were selected at random for harvest of root material. Roots were clipped from the shoots and washed. All plants were then individually dried at 100°C for 24 hours, and the weights recorded.

Statistical analysis of total plot yields included estimation of some missing row data by a method developed by Yates (1933). Intra-plot analysis involved yields of respective species within different

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spatial patterns. Treatments were defined by which competing species made up rows on either side of the species under analysis. In this analysis, only rows that were in between two rows of similar species were used. Any row that was in between two rows of different species was not considered for analysis. Statistical analysis of this portion of the experiment involved a two-level nested analysis of variance with unequal sample sizes.

Competitive Ability Experiment

Experiment II was designed to determine, in a paired-species manner, the relative ability of the four species to compete. The basic experimental design employed was a randomized block with five treatments - competition from each of the four species plus a control. Each sample plant was ringed by six treatment plants that were equidistant (15 cm) from the sample (target) plant, as well as from themselves. This hexagonal pattern was also used by Goodall (1960), Harper (1961) and Sakai (1965) in similar experiments. Control plants were sown singly, without neighbors.

Interference stress criteria were root and shoot weights attained when species were subjected to both intra- and interspecific competition. Treatment effects were compared through use of a least significant range test. Field preparation was the same as in Experiment I. Polyethylene templates were used for the first five weeks to maintain experiment patterns and the plots were watered every three days. Drying and weighing were accomplished in the same manner as in Experiment I. Species were ranked as to their competitive abilities, based on yields attained under competitive stress from the other

species. This ranking was compared to yields of each species in different mixtures in the first experiment.

RESULTS

Experiment I - The Diversity-Yield Plots

Once the seedlings germinated, the dicots, Amaranthus and Chenopodium, were the fastest growing plants in the mixture plots. By the fifth week, based on observation in the field, it appeared that Amaranthus was the dominant component in the mixture plots, while Chenopodium was the second most productive. The crown of Chenopodium tended to be more cylindrical than that of Amaranthus which was wider and tapered toward the top. With regard to roots, Amaranthus exhibited a dominant central tap root while Chenopodium had a root system composed of several robust branch roots. Crown structure of the two grasses did not differ greatly. Their root systems were shallow and fibrous, with those of Setaria being more coarse than those of Panicum.

Mean total shoot yield per plot ranged from a high of 4090.65 grams in pure stands of Amaranthus to the lowest yield of 2368.25 grams in Setaria monocultures (Figure 2). Analysis of variance indicated significant differences among treatments at the 95% level (Table 1). Pure stands of Amaranthus produced yields that were significantly greater than those of the Setaria monocultures. Although yields of monocultures of Amaranthus were consistently greater than those of the other treatments also, the difference was not significant ($\alpha = 0.05$). In pure stands, ranking of yield per species was, from highest

Figure 2. Mean yields of total above ground biomass per plot in the diversity-yield experiment. Letters in parentheses represent which species are interspaced in that particular plot. (PACS), for instance, indicates that Panicum and Amaranthus are side by side and Chenopodium and Setaria are side by side. Circles are the grand means and the vertical bars are $\pm$ one standard error.

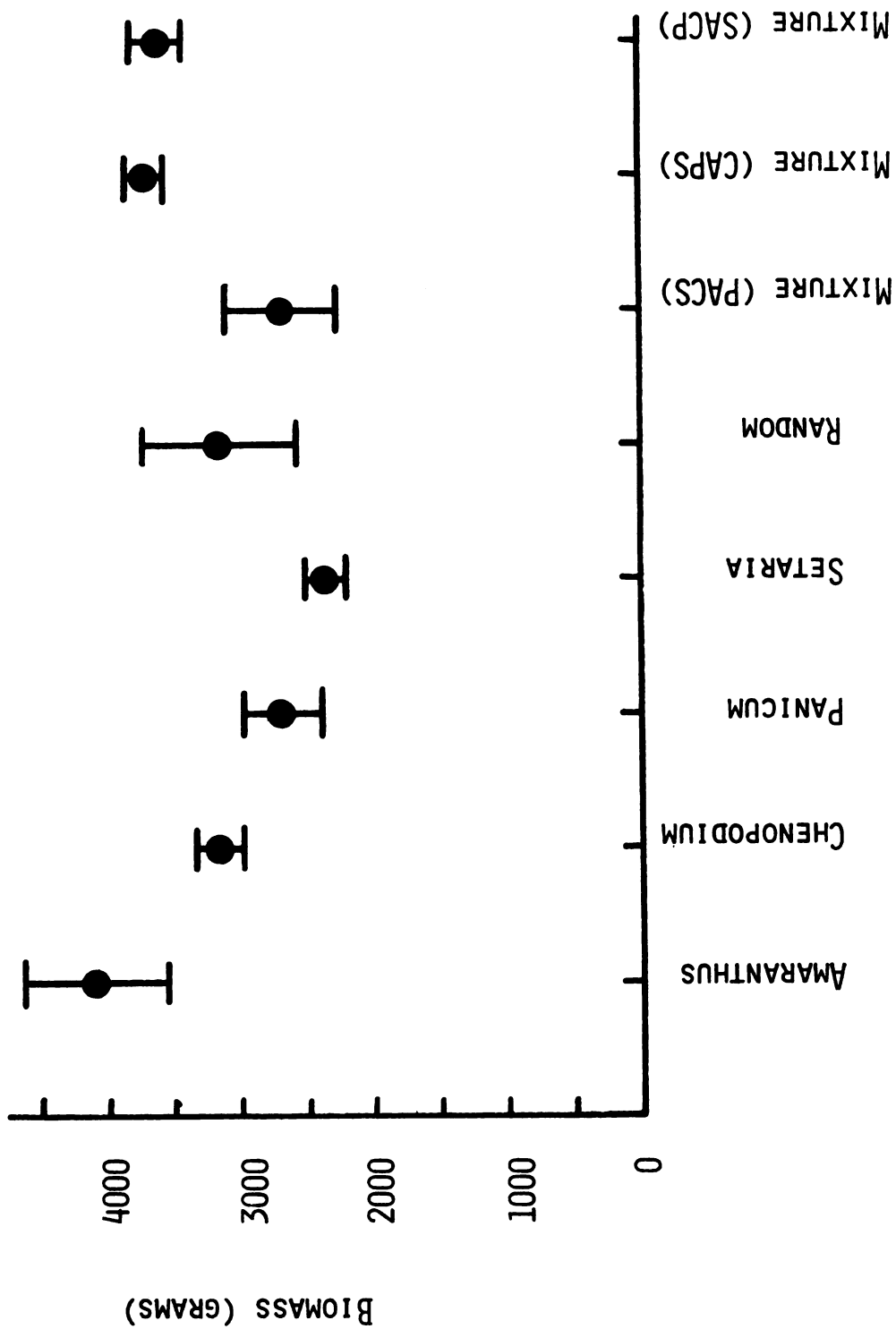


FIGURE 2

Table 1. Mean yield per plot of treatments in experiment I, the diversity-yield experiment.

Plant Array	Mean Yield/Plot (grams)	S.E.	Metric Ton/Hectare	Tons/Acre
<u>Amaranthus</u>	4090.65 ^a	± 531.06	1.64	0.73
Mixture (CAPS)	3701.90 ^{ab}	± 137.72	1.48	0.66
Mixture (SACP)	3601.90 ^{ab}	± 192.39	1.44	0.64
<u>Chenopodium</u>	3168.31 ^{ab}	± 175.61	1.27	0.57
Random	3154.35 ^{ab}	± 579.59	1.26	0.56
<u>Panicum</u>	2691.13 ^{ab}	± 286.60	1.08	0.48
Mixture (PACS)	2683.70 ^{ab}	± 416.07	1.07	0.48
<u>Setaria</u>	2368.25 ^b	± 146.63	0.95	0.42

Sets of means sharing a common subscript are not significantly different ($\alpha = 0.05$).

to lowest, Amaranthus, Chenopodium, Panicum and Setaria. The analysis of variance table and least significant range table are in Appendix A-1.

Relative contributions to mixture plot yield by the component species exhibit definite and repeatable trends. Hierarchy of relative contributions to yields of mixture plots was Amaranthus > Chenopodium > Setaria > Panicum, except in the mixture plot (SACP) where Panicum contributed more above ground yield to the array than Setaria (Figure 3).

Within the plots, Amaranthus was generally the best competitor while Setaria was the poorest (Figures 4-5). Lowest shoot yields per row occurred when the species were between two rows of Amaranthus. Significantly higher shoot yields per row were attained when they were interfaced with the grasses. Chenopodium had a significantly greater effect than Panicum on repressing shoot yields of all species except Amaranthus. There was no difference between effects of Panicum or Chenopodium on the mean yield of Amaranthus (Figure 6). Analysis of variance tables are in Appendix A-2.

Mean root yields of species within plots, except for Amaranthus were significantly lower when subjected to competition from the dicots as compared to the effect of the grasses. Relative root yields are shown in Figures 7 and 8 and statistical relationships are represented in Figure 9. Analysis of variance tables are in Appendix A-3.

Experiment II - Competitive Ability

In all cases, the dicots, Chenopodium and Amaranthus, were the most effective competitors (Figures 10 - 13). Target plants of all species attained the least shoot yield when surrounded by either of the dicots. In all cases, the dicots were stronger competitors than

Figure 3. Relative contributions to total plot yields by component species of the mixture plots in the diversity-yield experiment.

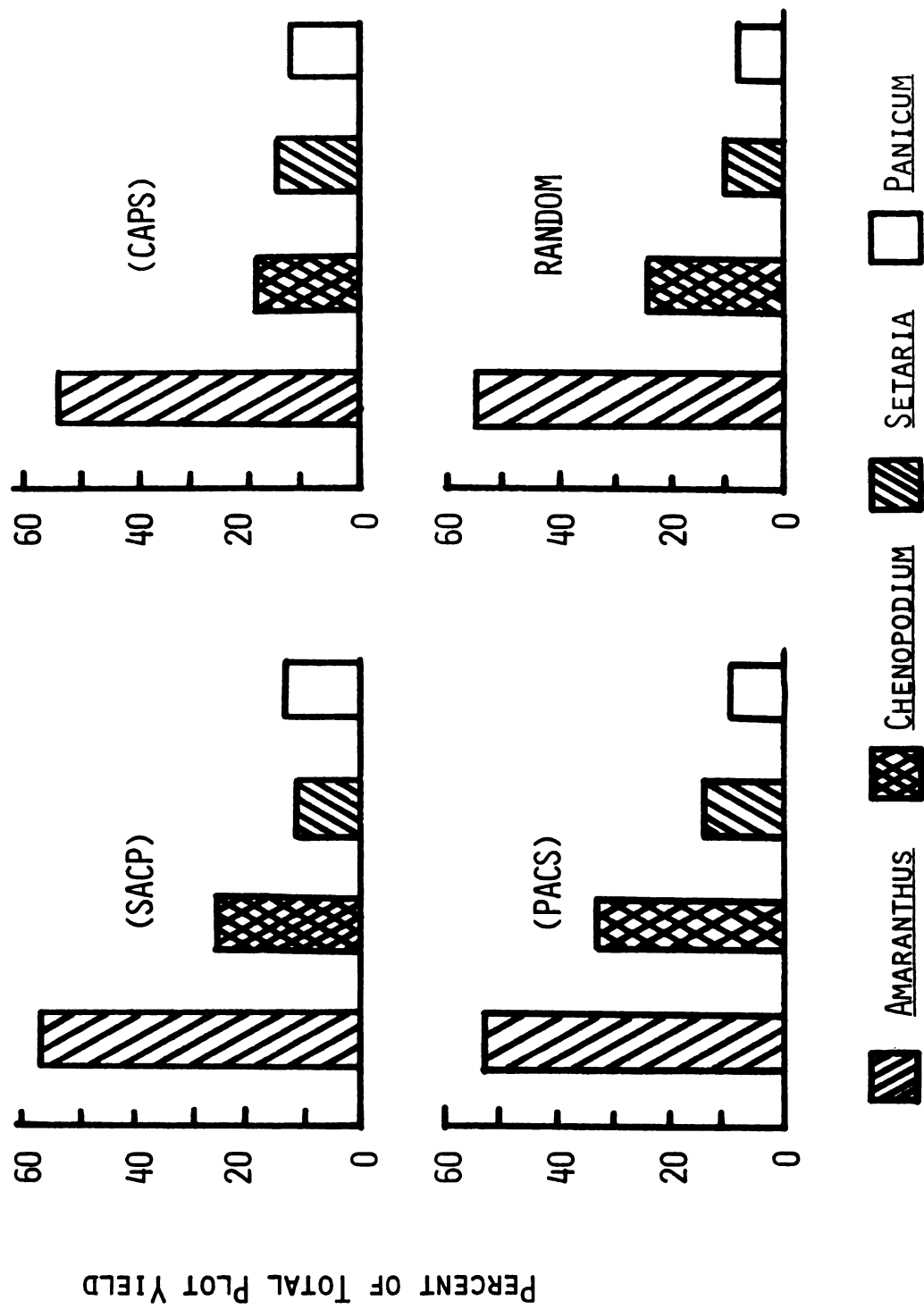


FIGURE 3

Figure 4. Mean yield per row of Amaranthus (▲) and Chenopodium (●) when flanked by two rows of each of the mixture plot components.

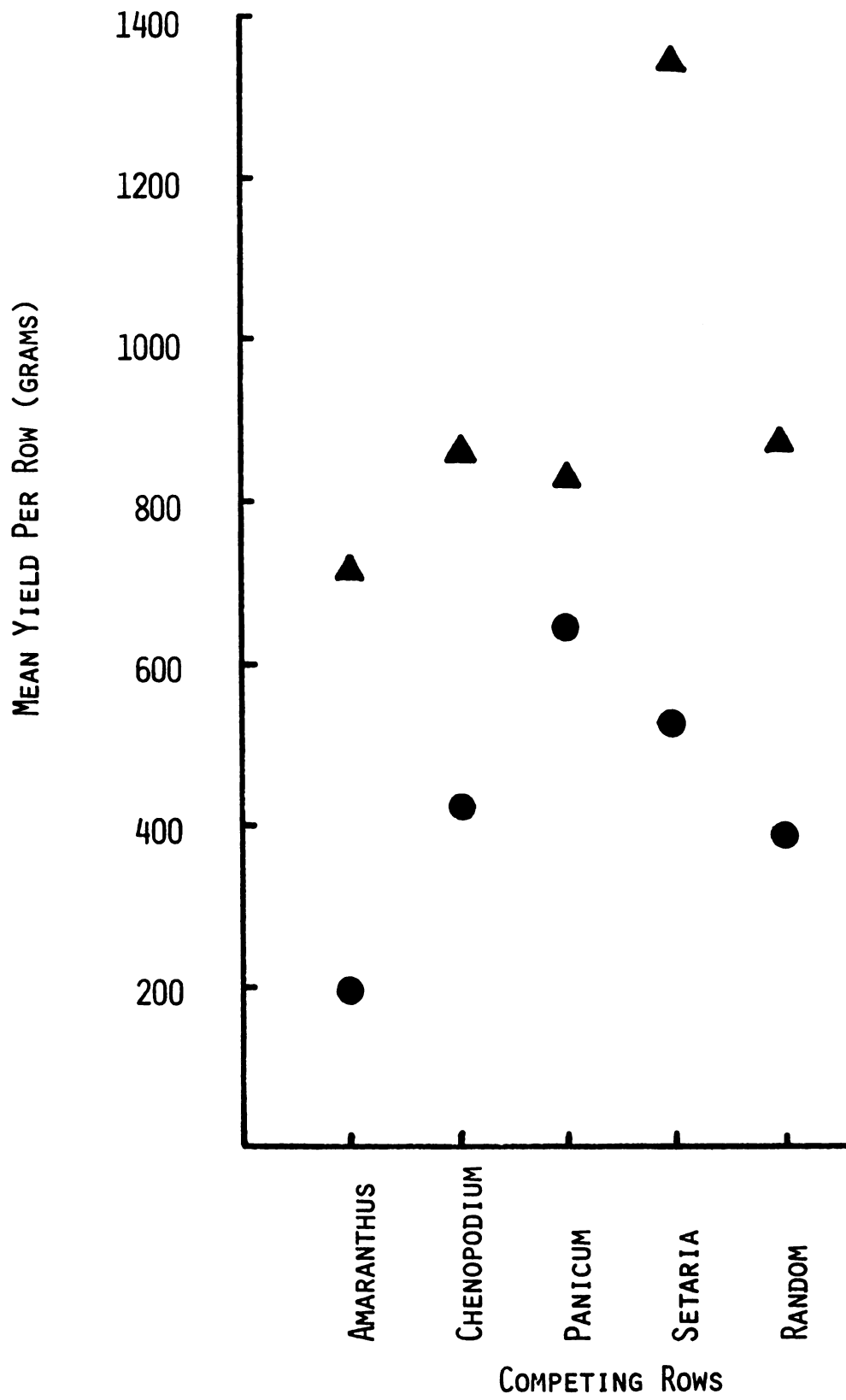


FIGURE 4

Figure 5. Mean yield per row of Panicum (▲) and Setaria (●) when flanked by two rows of each of the mixture plot components.

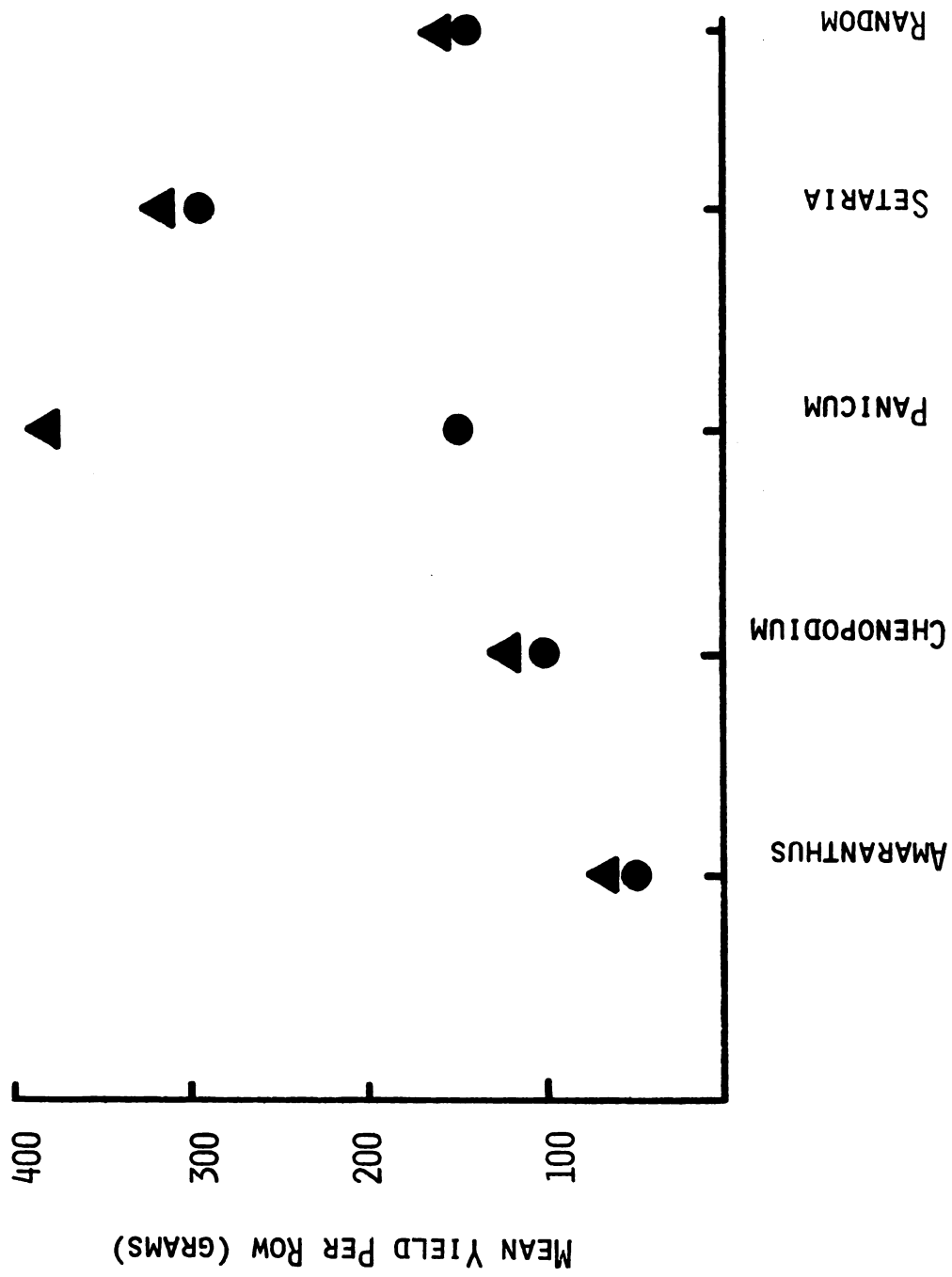


FIGURE 5

COMPETING ROWS

Figure 6. Diagrammatic representation of statistical differences in mean shoot yields per row of diversity-yield plot species when interfaced by rows of different competitors. Underlining represents those sets of means not significantly different. Any two means not connected by a line are considered significantly different at the 95% level.

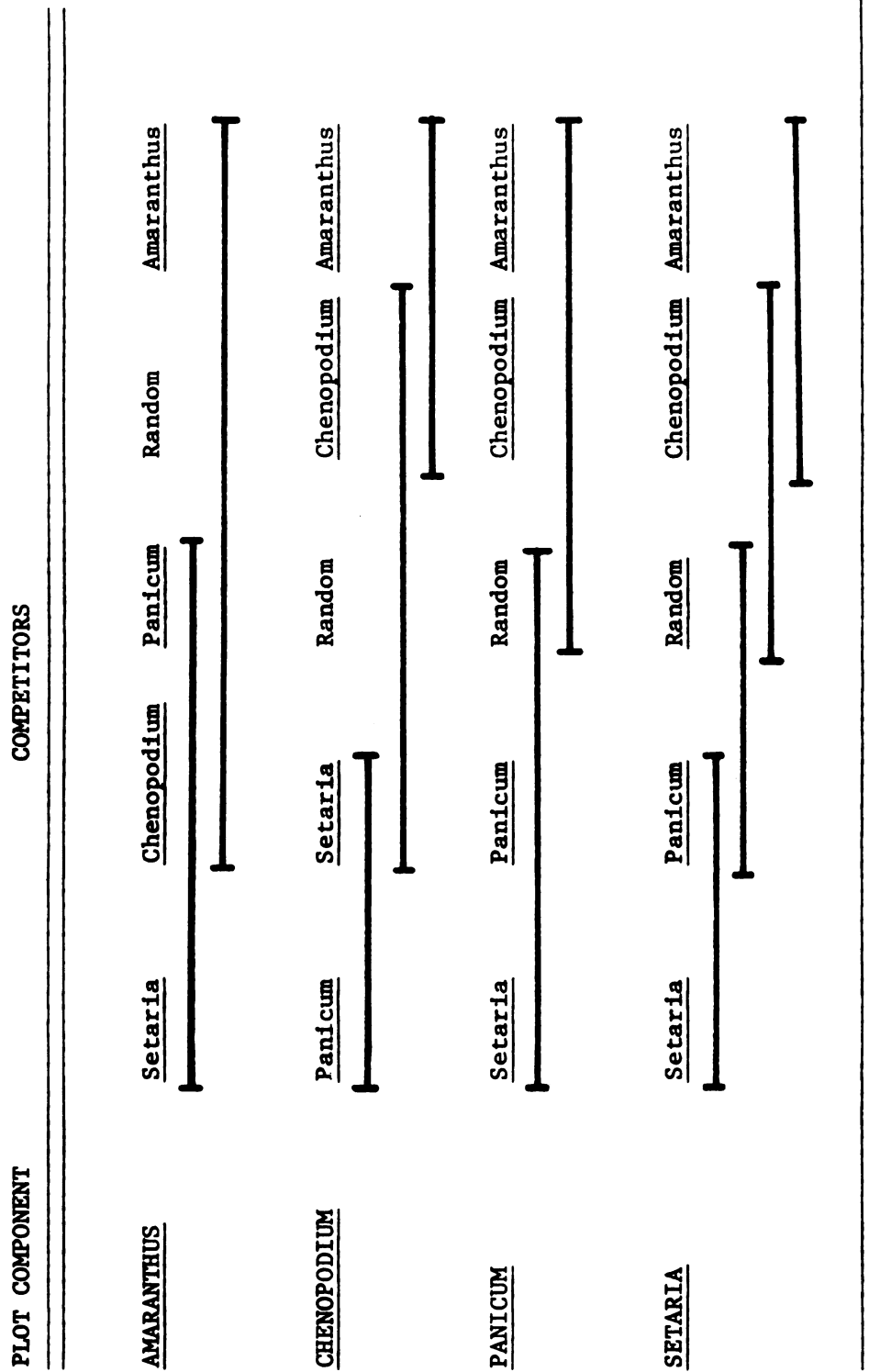


FIGURE 6

Figure 7. Estimated mean root yield/row of Amaranthus and Chenopodium when between two rows of each of the other mixture plot species.

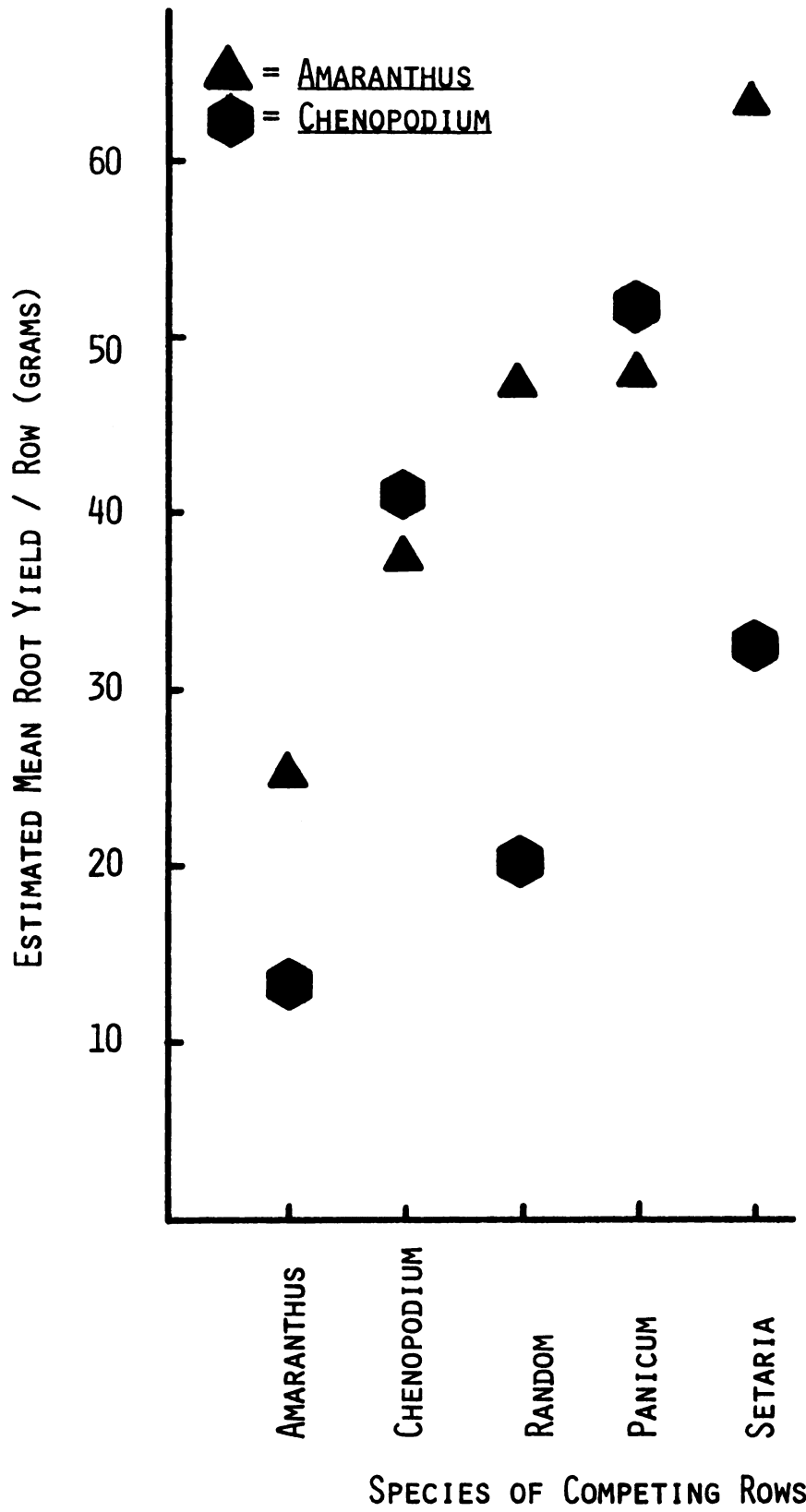


FIGURE 7

Figure 8. Estimated mean root yield/row of Panicum and Setaria when between two rows each of the other mixture plot species.

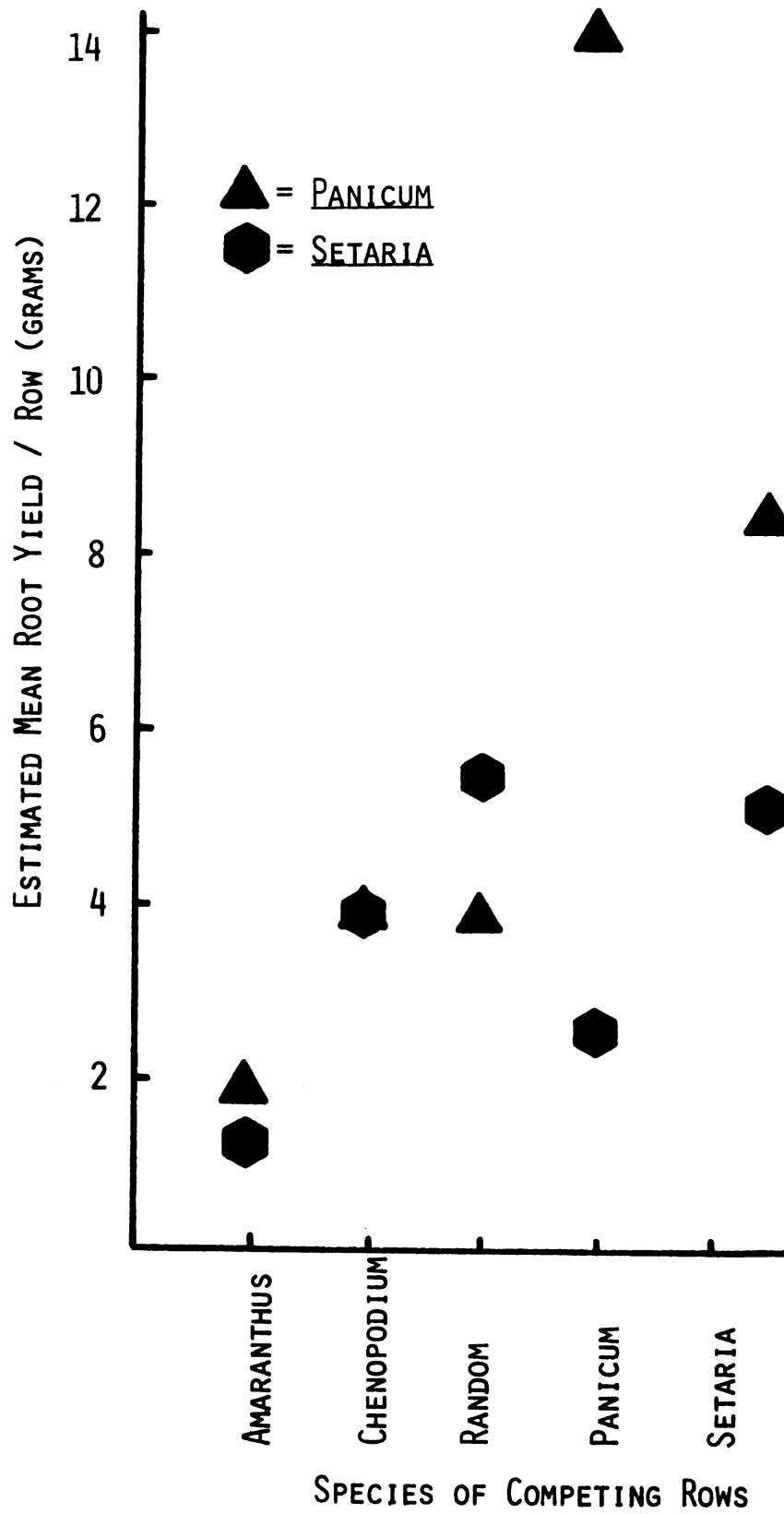


FIGURE 8

Figure 9. Diagrammatic representation of statistical differences in mean root yields of diversity-yield plot species when interfaced with different competitors. Underlining represents those sets of means not significantly heterogeneous. Any two means not connected by a line are considered significantly different at the 95% level.

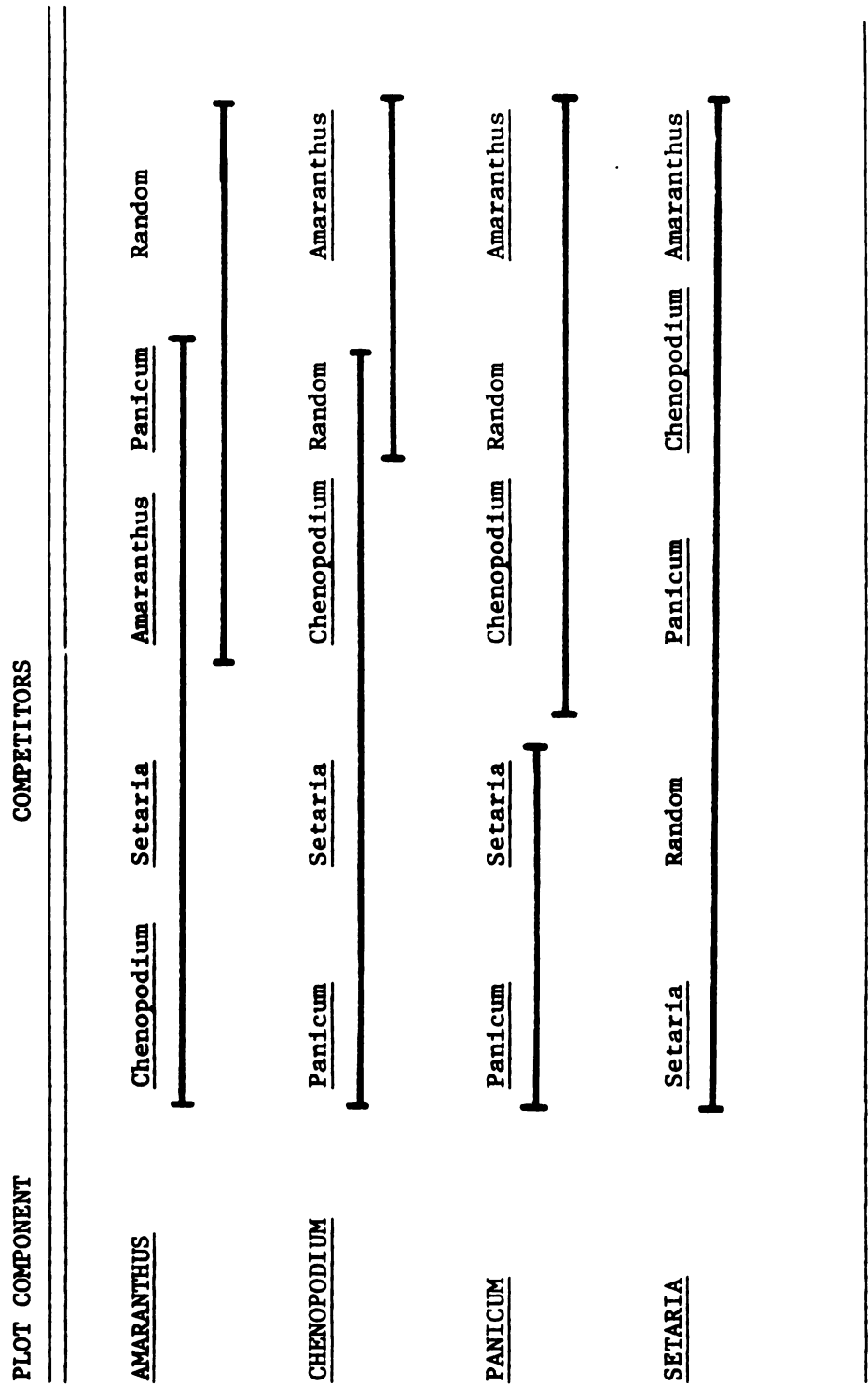


FIGURE 9

Figure 10. Mean shoot yield of Amaranthus target plants when encircled by intra- and interspecific competitors. Vertical bars represent $\pm$ two standard errors.

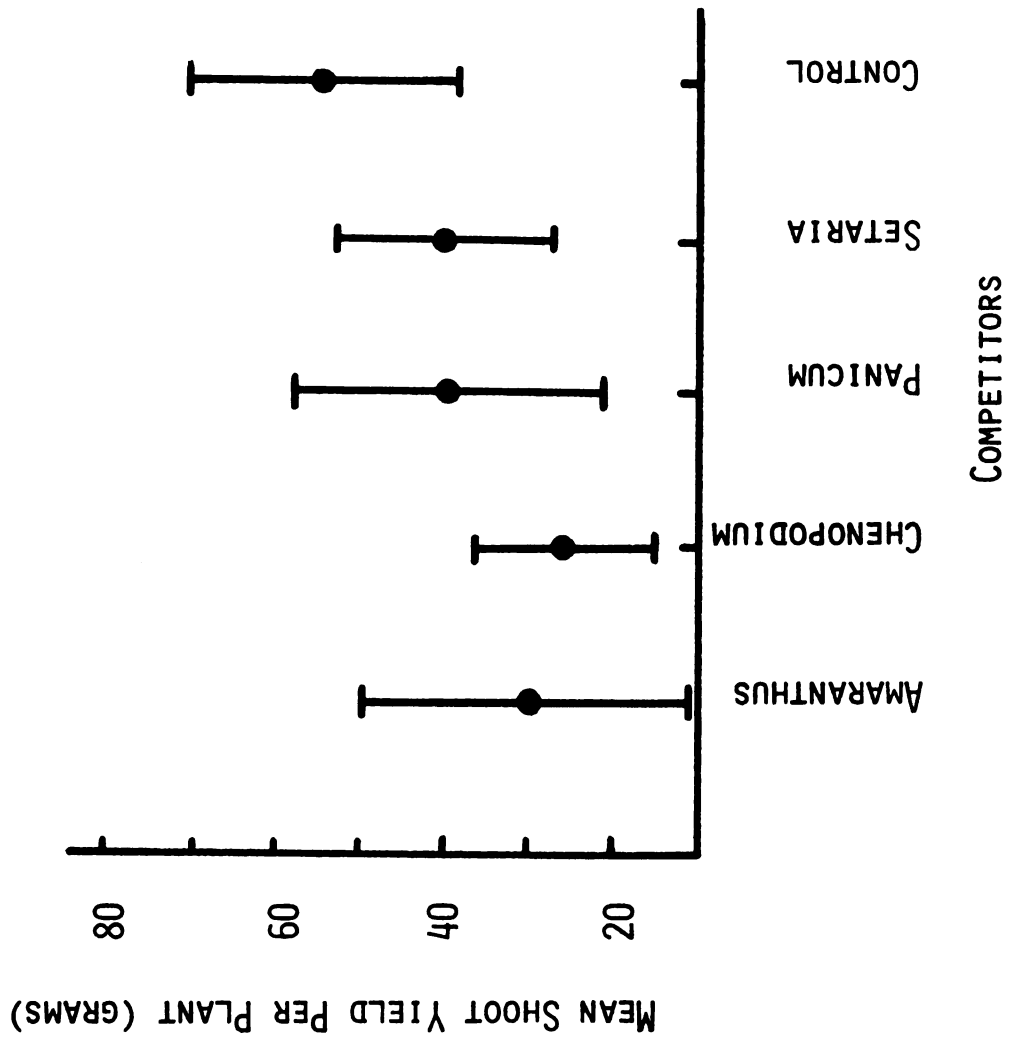


FIGURE 10

Figure 11. Mean shoot yield of Chenopodium target plants when encircled by intra- and interspecific competitors. Vertical bars represent two standard errors ($\pm$).

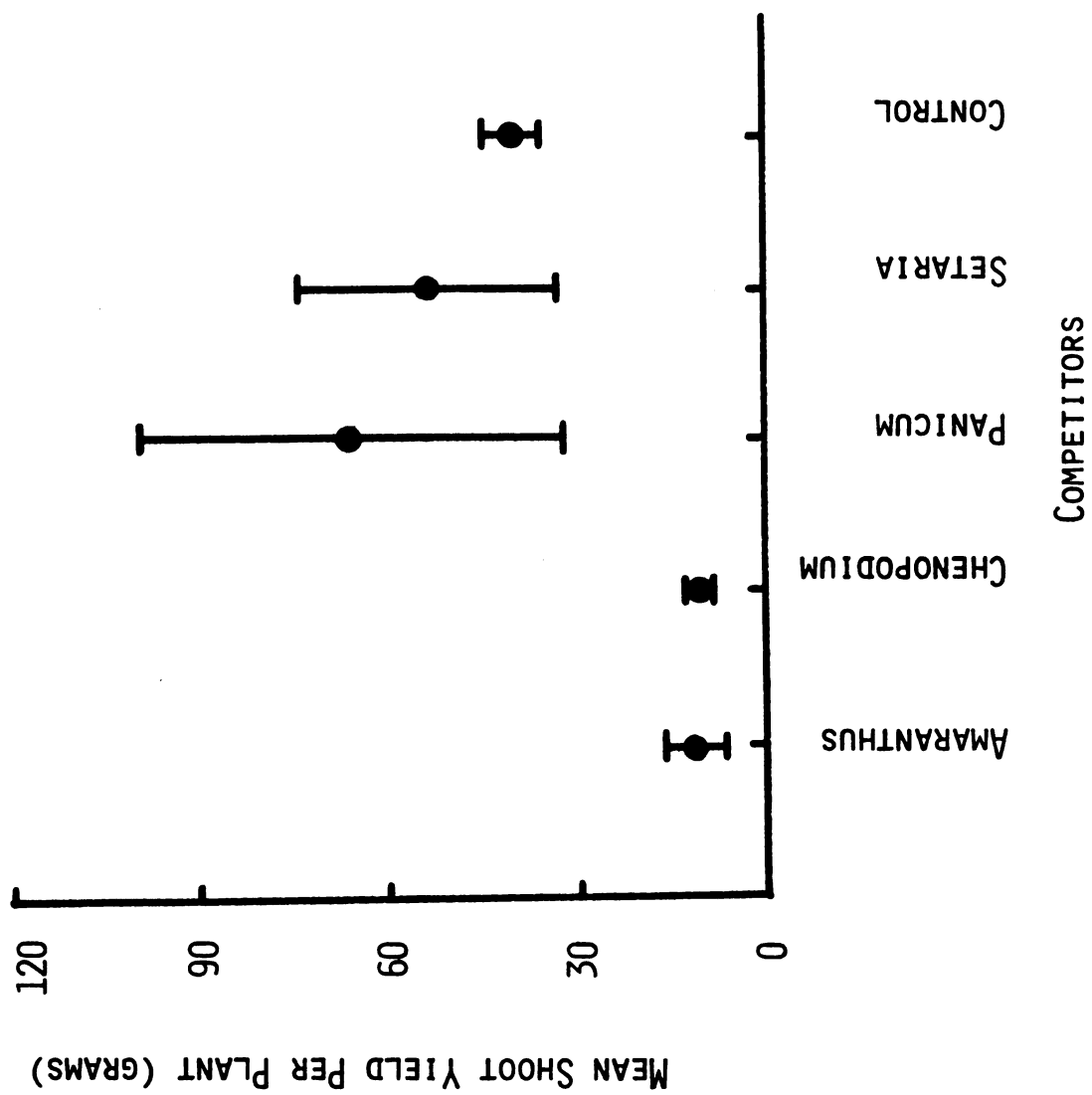


FIGURE 11

Figure 12. Mean shoot yield of Panicum target plants when encircled by inter- and intraspecific competitors. Vertical bars represent $\pm$ two standard errors.

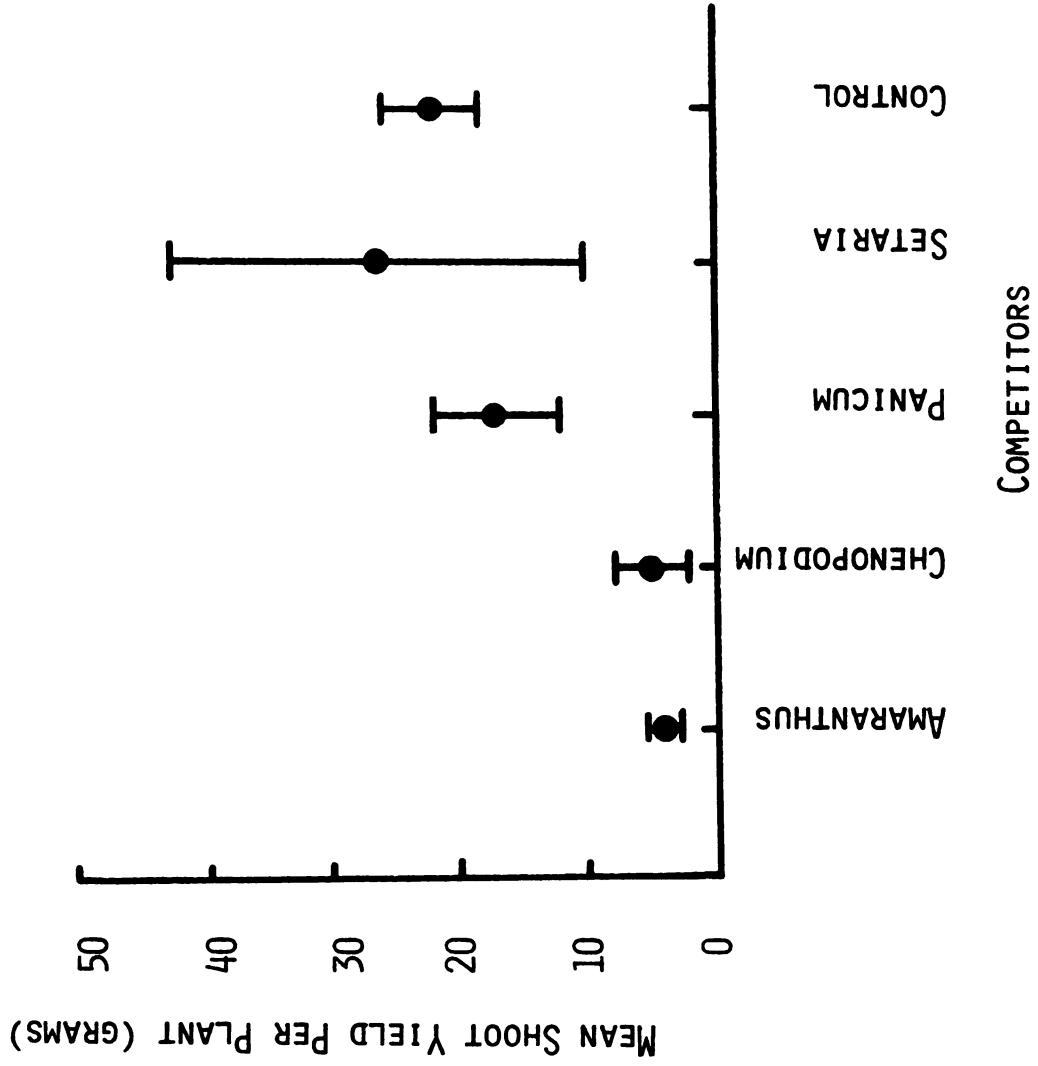


FIGURE 12

Figure 13. Mean shoot yield of Setaria target plants when encircled by intra- and interspecific competitors. Vertical bars represent $\pm$ two standard errors.

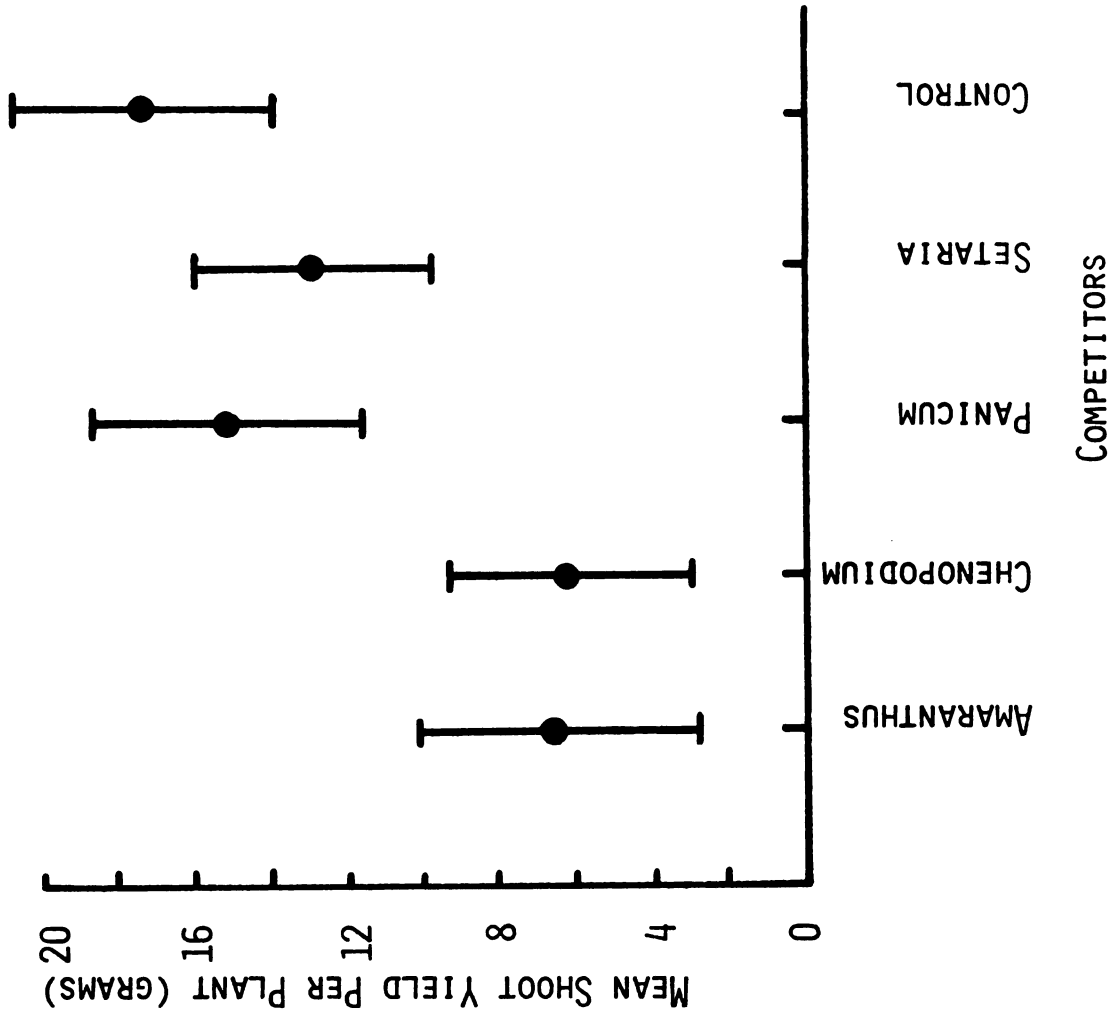


FIGURE 13

the grasses. The statistical relationships of "target" plant shoot yields under different treatments are shown in Table 2.

As with the shoots, the root yields of "target" plants of all species were repressed more by the dicots, Amaranthus and Chenopodium, than by the grasses (Figures 14 - 17). In each case, root yields of "target" plants surrounded by either of the dicots, were not significantly different (Table 3). Similarly, the effects of the competitor rings of either Panicum or Setaria on root yields of all species were not significantly different. Analysis of variance tables and least significant range tables are in Appendix A-5.

Table 2. Mean shoot weight of target plants in Experiment II when surrounded by intra- and interspecific competitors.

Competitors	Target Plants							
	<u>Amaranthus</u>		<u>Chenopodium</u>		<u>Panicum</u>		<u>Setaria</u>	
	Ave. wt.	SE	Ave. wt.	SE	Ave. wt.	SE	Ave. wt.	SE
<u>Amaranthus</u>	19.49 _{ab}	10.14	11.18 _a	2.09	3.72 _a	0.64	6.88 _{ab}	1.82
<u>Chenopodium</u>	14.83 _{ab}	4.88	10.90 _a	0.94	5.53 _a	1.38	6.13 _a	1.65
<u>Panicum</u>	39.18 _{bc}	11.99	66.07 _c	16.86	17.04 _b	2.35	15.11 _c	1.78
<u>Setaria</u>	39.66 _{bc}	8.39	53.34 _{cb}	10.30	23.71 _b	6.9	12.99 _{bc}	1.57
Control	58.77 _c	10.72	40.48 _{bc}	4.62	22.48 _b	2.11	17.60 _c	2.28

Means are not significantly different if they are followed immediately by the same small letter.

Figure 14. Mean root yield of Amaranthus target plants when encircled by intra- and interspecific competitors. Vertical bars represent $\pm$ two standard errors.

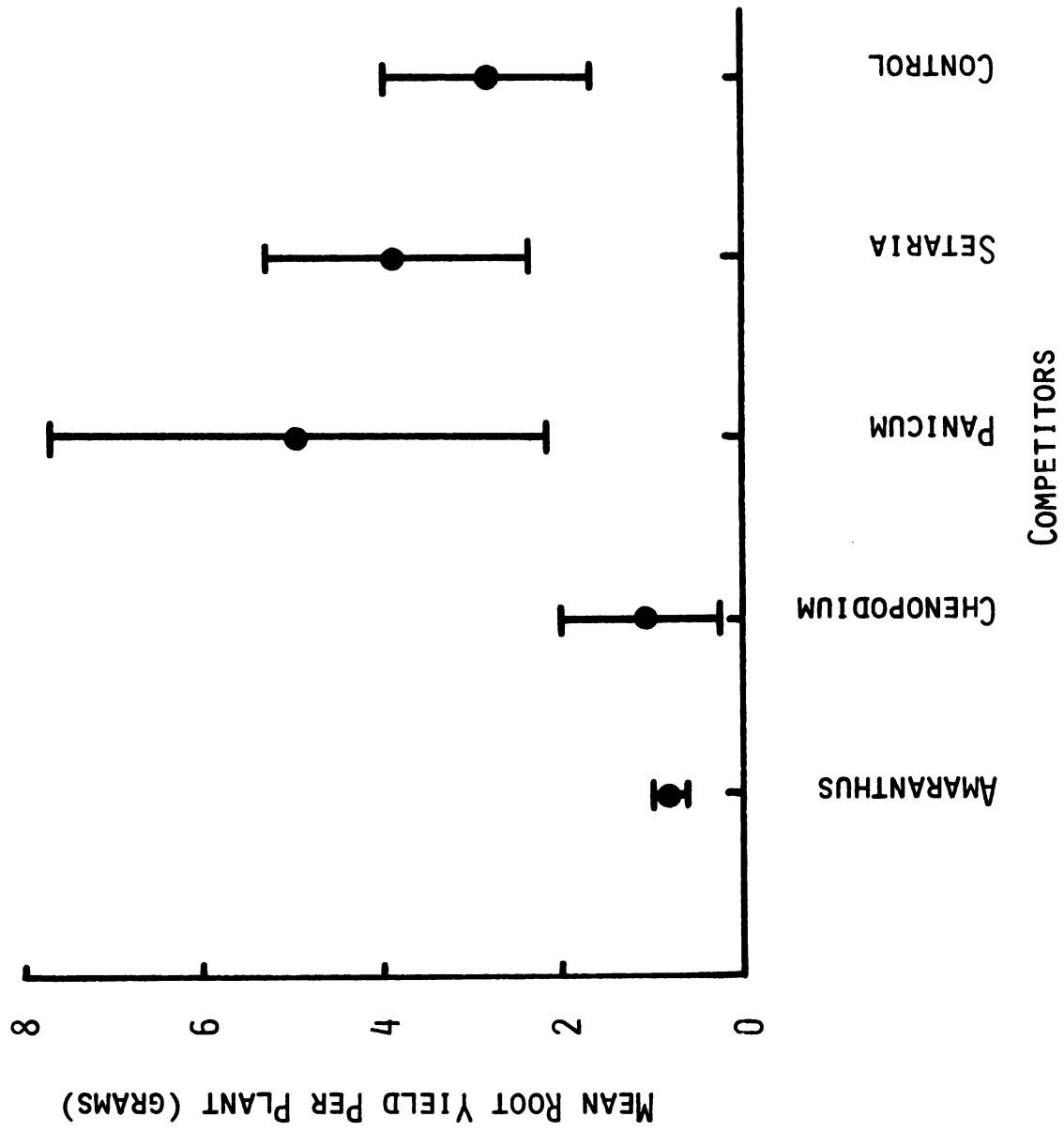


Figure 15. Mean root yield of Chenopodium target plants when encircled by intra- and interspecific competitors. Vertical bars represent $\pm$ two standard errors.

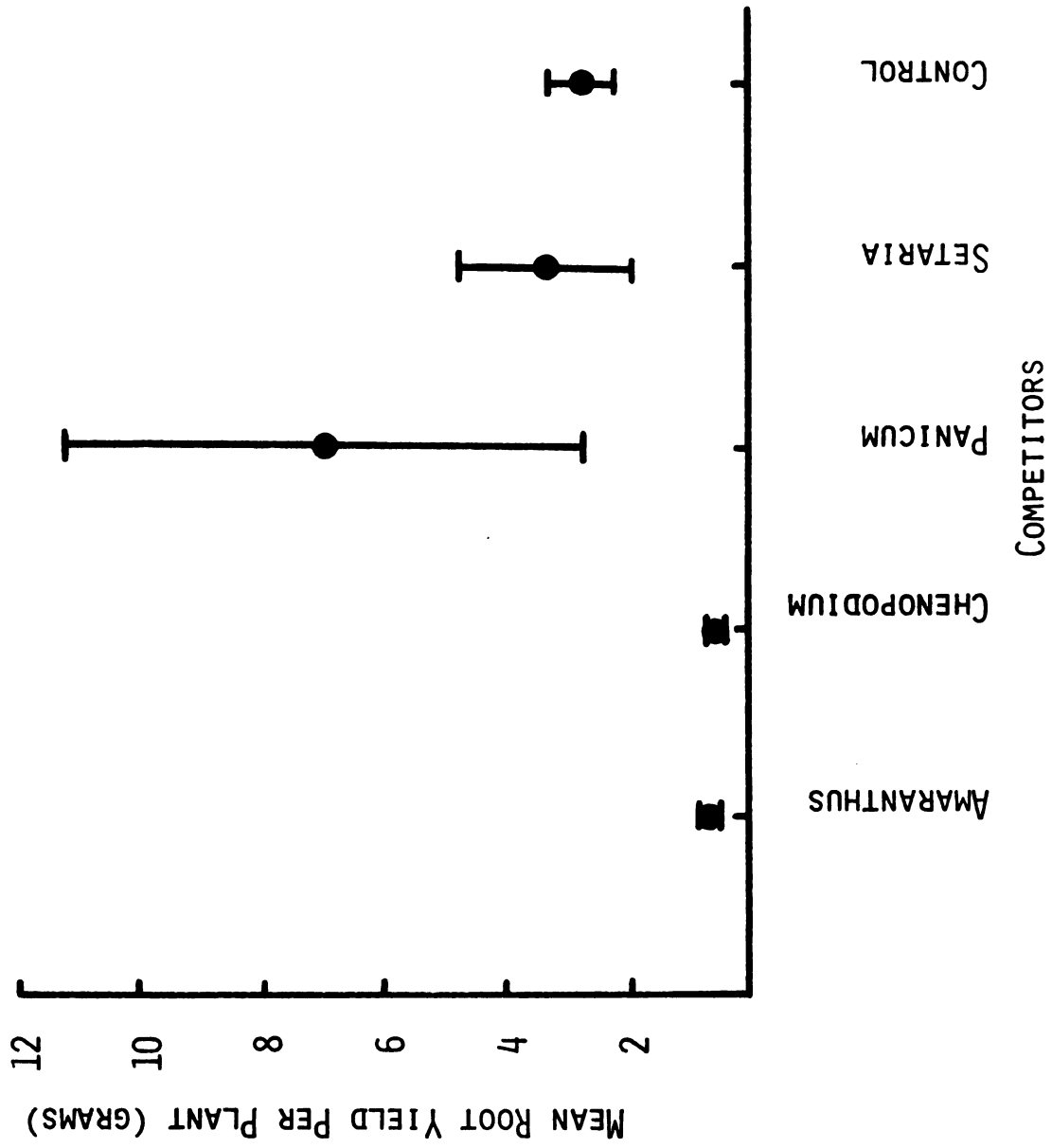


FIGURE 15

Figure 16. Mean root yield of Panicum target plants when encircled by intra- and interspecific competitors. Vertical bars represent $\pm$ two standard errors.

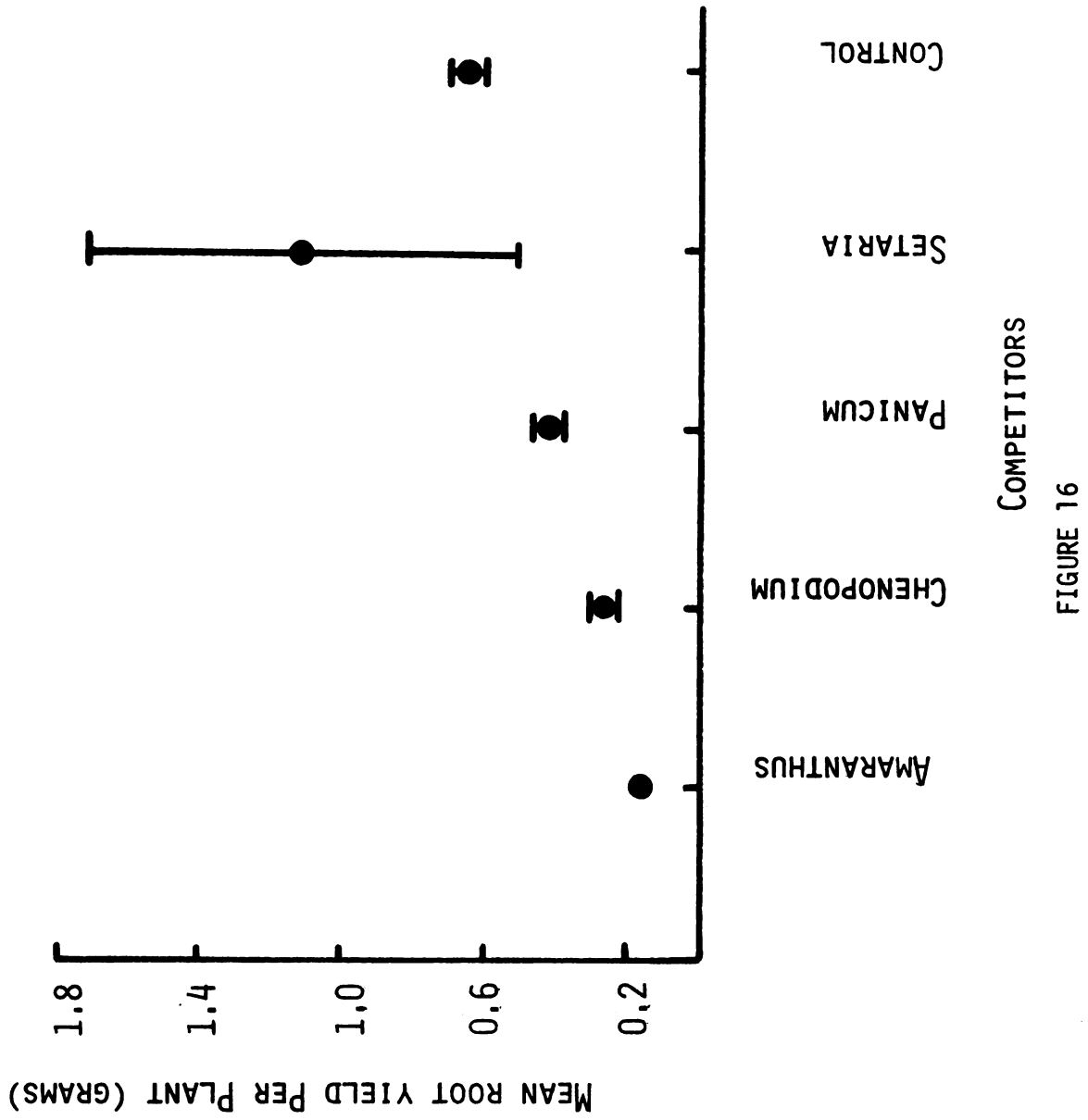


Figure 17. Mean root yield of Setaria target plants when encircled by intra- and interspecific competitors. Vertical bars represent $\pm$ two standard errors.

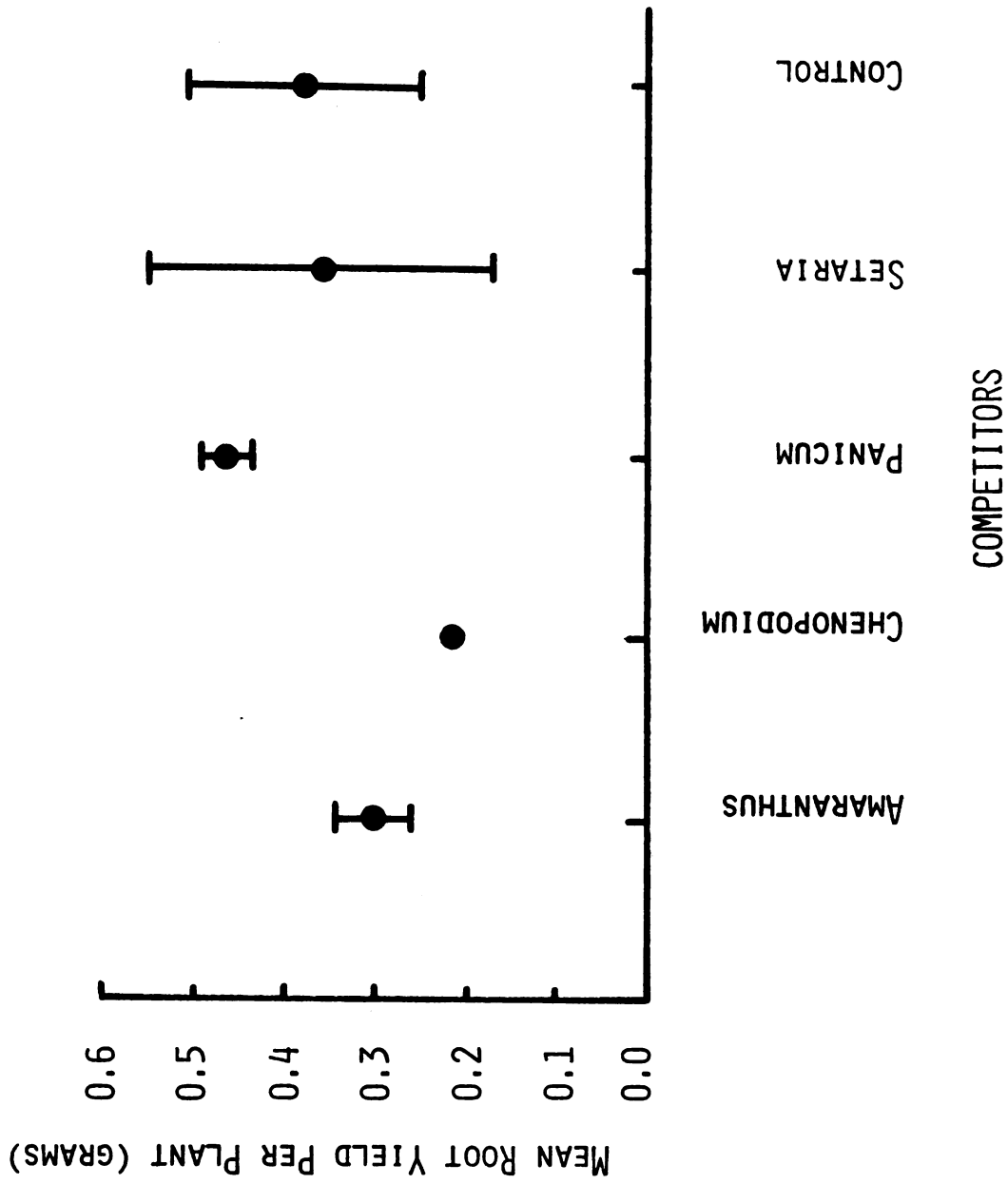


FIGURE 17

Table 3. Mean root weights of "target" plants in Experiment II when surrounded by intra- and interspecific competitors.

Competitors	Target Plants							
	<u>Amaranthus</u>		<u>Chenopodium</u>		<u>Panicum</u>		<u>Setaria</u>	
	Ave. wt.	SE	Ave. wt.	SE	Ave. wt.	SE	Ave. wt.	SE
<u>Amaranthus</u>	0.87	a	0.60	a	0.15	a	0.28	ab
<u>Chenopodium</u>	0.35	a	0.58	a	0.23	a	0.21	a
<u>Panicum</u>	4.36	a	7.05	b	0.42	ab	0.47	b
<u>Setaria</u>	3.45	a	3.87	b	0.96	b	0.38	ab
Control	2.78	a	3.06	ab	0.66	b	0.44	ab

Means are not significantly different if they are followed immediately by the same letter.

DISCUSSION

Diversity versus Yield

One of the primary objectives of this study was to determine whether a mixture of different species can better exploit the resources of a particular site than pure stands of the component species of the mixture; in other words, whether diversity, in a given system, is related to NPP in a positive way. The experimental variables were diversity and plant array patterns. Site potential (nutrients, water, etc.) was held constant and treatment effect was gauged by the magnitude of the resultant yield at the end of the growing season. Plant species incorporated in this study normally coexist in natural plant communities. Further, the experimental plants were grown under natural field conditions, as opposed to other mixture-yield studies (Bornkhamm, 1961; Haizel, 1972) in which potted plants, grown in greenhouse conditions, were used. It is for the above reasons that I feel results of this study can be extrapolated to actual field dynamics of the species used.

Although results of experiment I showed that mean yield per plot of pure stands of Amaranthus (4090.65 grams) was consistently greater than mean yields of any of the mixture treatments, statistically, there was no significant difference. Lowest mean yield per plot was that of Setaria (2368.25 grams) in monoculture. Thus mixture yields were comparatively lower than that of the highest yielding monoculture

(Amaranthus) and comparatively higher than the mean yield of the lowest yielding monoculture (Setaria). These results concur with those of Bornkhamm (1961) and Haizel (1972), with regard to the inability of mixtures to out-yield the highest yielding monoculture. It should be noted that although the mean yield per plot of pure stands of Amaranthus was higher than those of all other treatments, in a statistical sense, it did not have a significantly higher ($\alpha = 0.05$) yield than any of the other treatments except for pure stands of Setaria.

Perhaps life form differential among the component species used in this study was not sufficient to allow them to exploit site resources in different ways. Even though the root growth patterns of the dicots and monocots differed significantly, they still penetrated to the same depth of the rhizosphere and presumably, therefore, acquired soil nutrients in the same area. In this respect, biennial or perennial species, representative of later successional stages might be better organisms for this type of study because they exhibit root systems that range from fibrous sub-surface roots in some grasses to deeply penetrating tap roots of some biennial and perennial dicots. Whittington and O'Brien (1968) feel that lack of diversity in root growth patterns of species in mixtures is the major reason that those mixtures fail to attain yields higher than the highest yielding monoculture of the component species.

Another possible reason for failure of the mixture plots to out-yield the highest yielding pure stand was due to the use of an arbitrarily chosen fixed-density. Presumably, the lowest density at which a species produces the maximum yield per unit area is species

specific. Determination of this density for each species could be accomplished experimentally and then used as a base line for the density of each species in mixture plots. In this way, mixture plots could be designed that would exhibit minimal intraspecific competition stress. Of course, utilization of species with different growth patterns would enhance the "combining ability" of the species through minimizing interspecific competition among the species.

Allocation of Biomass Among Species in the Mixture Plots

A good measure of how species utilize available resources is how the resultant yield is allocated among them. Since relative densities and frequencies of species in experiment I are all equal, the relative importance values among the species are equal to their relative yields. Distribution of their yields generally follows a geometric series pattern, indicating a strong expression of dominance within the arrays. In all mixture plots, except (CAPS), the distribution of total yield among the species is not significantly different than that predicted by a geometric series curve (Figures 18 - 21). Distributions were compared to that predicted by a geometric series with a Chi-square test, using an α of 0.05 (Appendix A-6). In the (CAPS) plot, Chenopodium was directly interfaced with Amaranthus and therefore was subject to relatively high competition stress. Although the distribution was not a geometric series, the hierarchy of relative yields was the same as in other plots. Overall, Amaranthus, the most dominant species, yielded about 55% of the total biomass, based on dry weight yield. Chenopodium, the second most dominant species, produced about half the remaining biomass or about 25% of the total. Finally, the two grasses each produced about 12% of the total yield (Table 4).

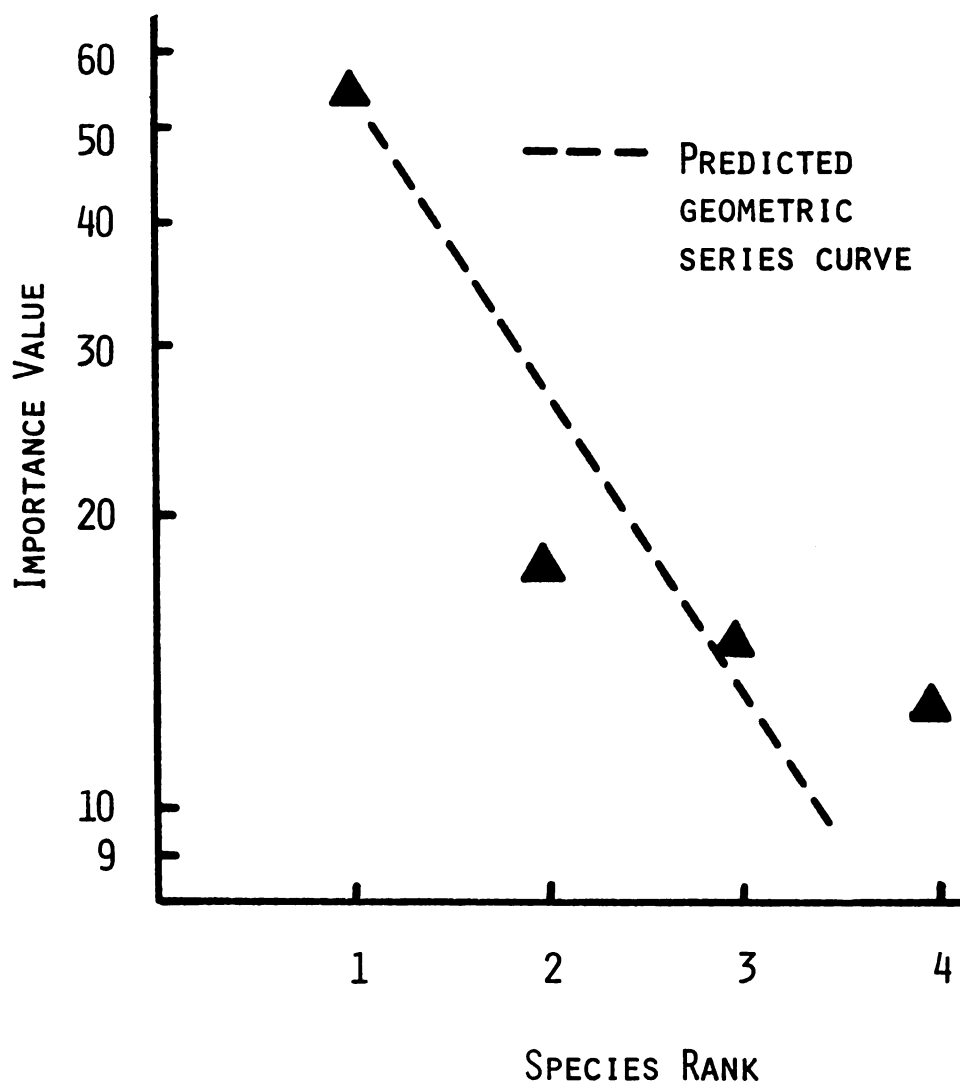


Figure 18. Distribution of importance values of the component species of mixture plot (CAPS).

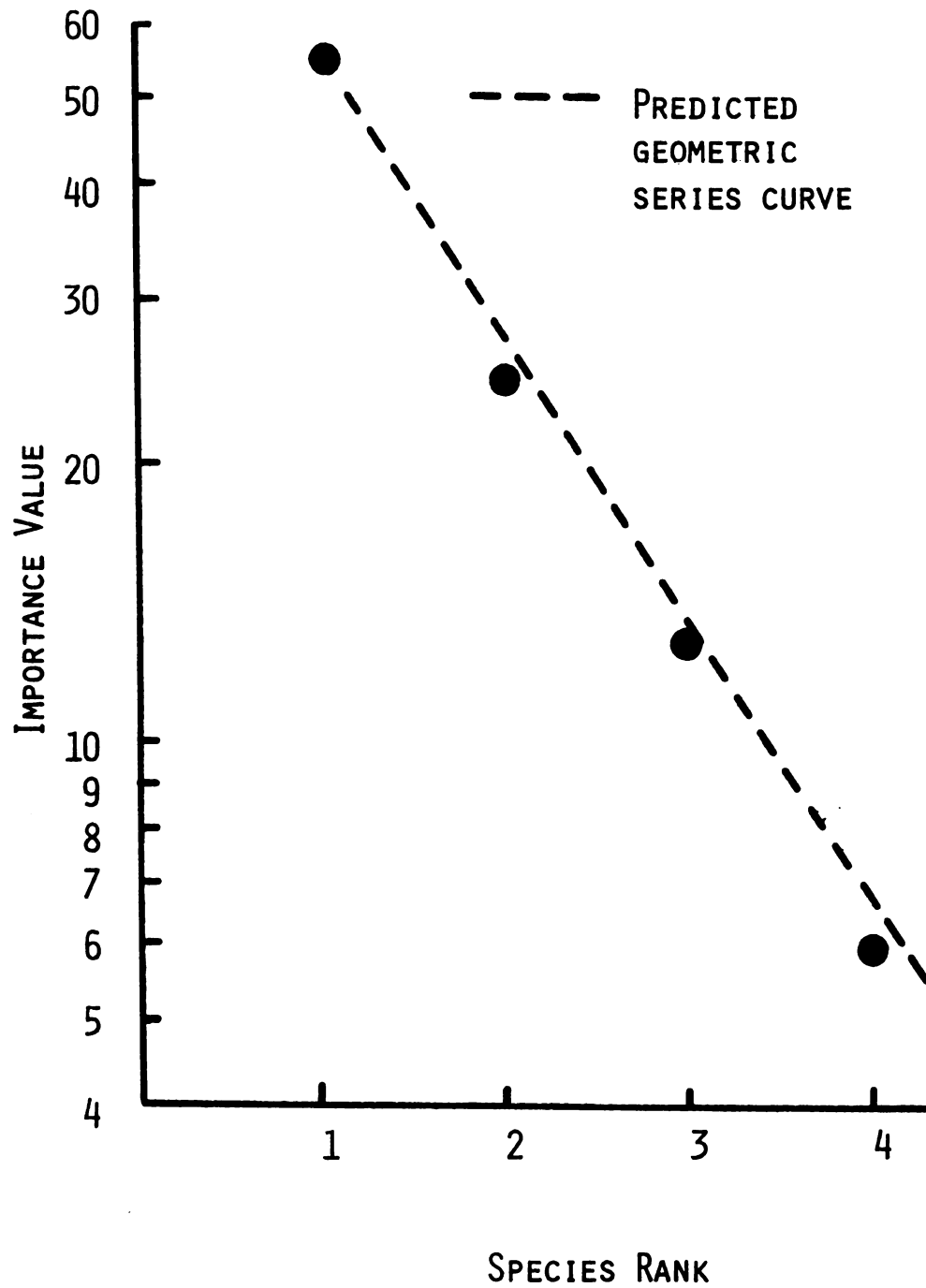


Figure 19. Distribution of importance values of the component species of mixture plot (SACP).

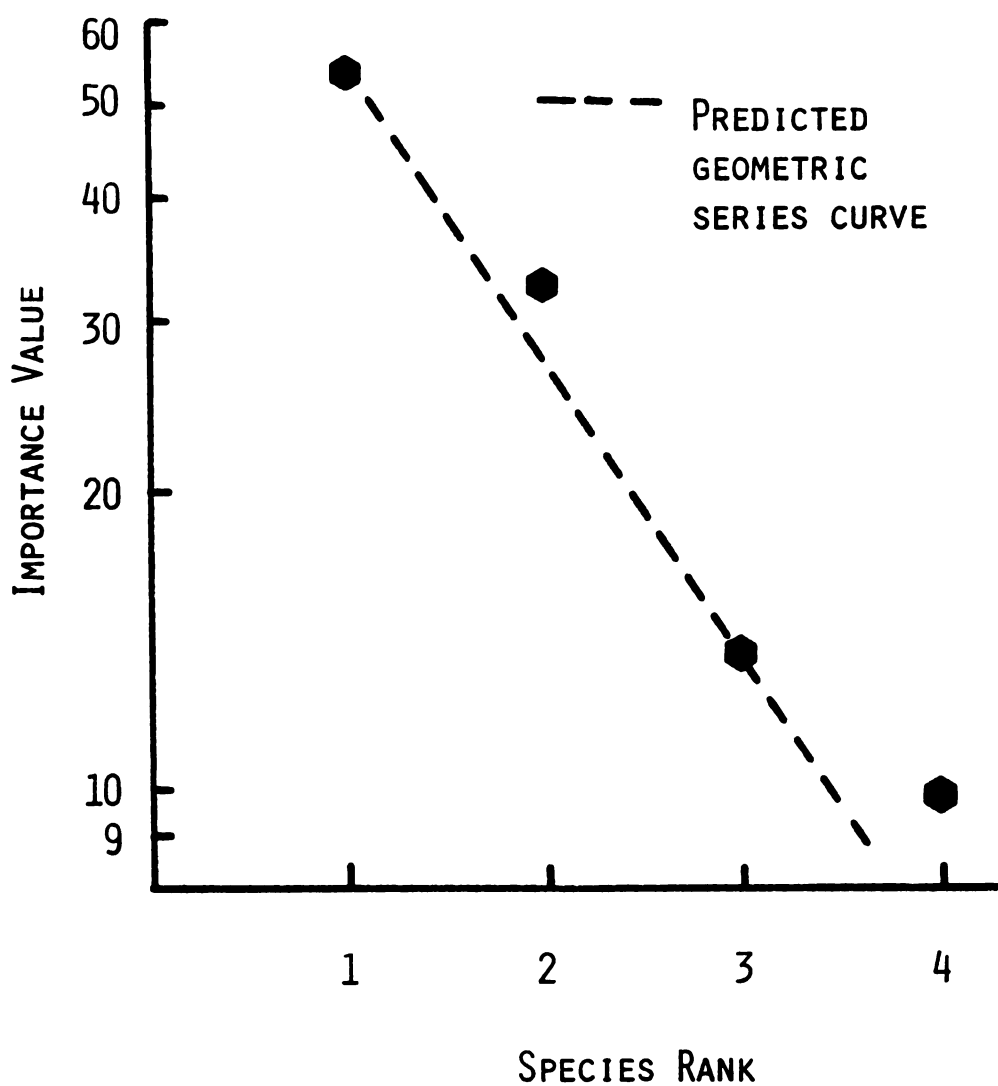


Figure 20. Distribution of importance values of the component species of mixture plot (PACS).

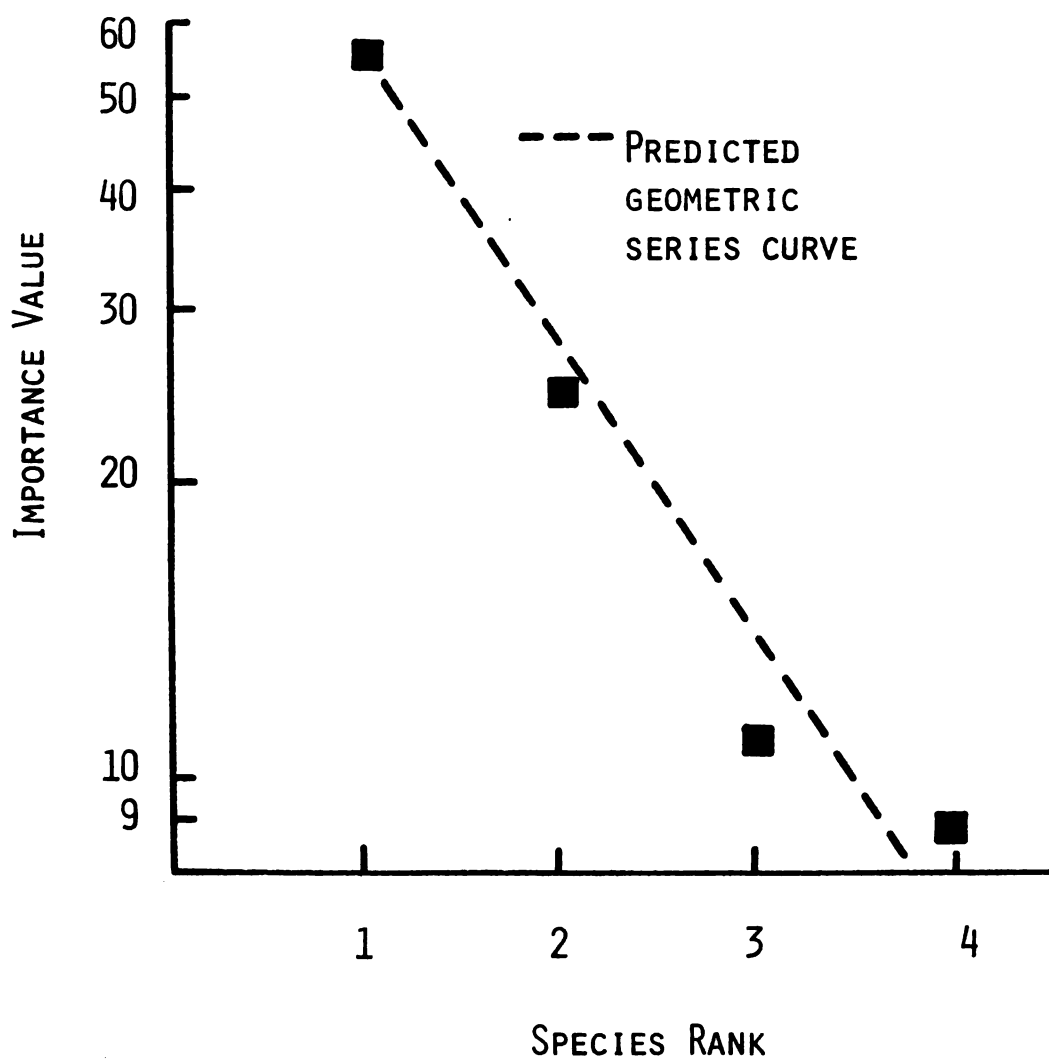


Figure 21. Distribution of importance values of the component species of mixture plot (RANDOM).

Table 4. Importance values of each species within the mixture plots.

Mixture Plot	Species		
	Amaranthus	Chenopodium	Setaria
Setaria-Amaranthus Chenopodium-Panicum	56	25	13
Chenopodium-Amaranthus Panicum-Setaria	54	18	13
Panicum-Amaranthus Chenopodium-Setaria	53	33	10
Random	55	25	9
Average	54.5	25.25	11.25

IMPORTANCE VALUE = (Species Yield per Plot/Total Yield per Plot) $\times$ 100

Allocation of site resources in a natural community can be expressed by the relative importance values of the component species. Distribution of the importance values is thought to be a direct indication of how they divide up the niche hyperspace of a community (Whittaker, 1970). The niche pre-emption hypothesis (Whittaker, 1965, 1969) states that the distribution will approach a geometric series. Communities in which dominance is strongly developed and the number of species is small usually exhibit this type of distribution. One example is the mid-Michigan first year old field community (Stephenson, 1973) in which Amaranthus, Setaria, Panicum and Chenopodium were strong dominants, in that order, based on their NPP.

It is interesting that a geometric series curve describes the allocation of site resources among the species in experiment I as well as among the species in the type of community where they occur in nature. The two grasses, Panicum and Setaria were both more dominant than Chenopodium in the natural community (Stephenson, 1973). Conversely, in the mixture plots of this study, Chenopodium was clearly dominant over the grasses. Constraints imposed by the design of experiment I such as holding the density and plant number per species constant as well as watering to augment natural precipitation, may have released Chenopodium from competition stress normally experienced in the fallow field community allowing it to increase its importance as a dominant species.

One constraint, with regard to my study, was the synchronous germination of the component species. I feel this germination synchrony was justified, with regard to the real fallow-field community, as the four species studied herein also germinated synchronously in the

fallow field on the periphery of my experimental plot. However, it would have been interesting to see how staggered sowing of the component species would have affected the relative contributions of the component species to total mixture plot yield.

Harper (1961), in a study with Bromus rigidus and B. madritensis, measured their relative yields in mixtures when each species was sown at different times. He found there was no detectable difference in total yield per pot of differently timed mixtures. However, relative contributions of each species to total yield was greatly altered. It is possible, therefore, that some other species, in my experiment, would have been dominant had the germination times of the component species not been synchronous. Whether the total yields of the mixtures would have been different, can only be answered through further studies.

In natural fallow-field communities, productivity of the whole system is allocated among component species in a temporal sense. Reed (personal communication), in a study on the productivity of a first year fallow-field community in mid-Michigan, demonstrated that the plant array contains functional groups, based on the type of photosynthetic pathways the plants possess and whether they are monocotyledonous or dicotyledonous plants that contribute differentially to the total array NPP throughout the season. Monocotyledonous plants possessing the C_3 -Calvin cycle photosynthetic pathway (cool season grasses) and dicotyledonous plants with the C_3 pathway are the major contributors to the productivity of the system during June and July. In late summer, dicots with the C_4 - dicarboxylic acid pathway of carbon fixation, are the dominant producers, with NPP rates five times greater than any other functional group. Finally, at season's

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end, between September and October, the perennial C_3 grasses exhibited a resurgence in NPP and subsequently produced biomass at a relatively high rate until late September when cool weather started to slow down the photosynthetic machinery.

Pattern versus Yield

Results of experiment I do not indicate that the net primary productivities of the mixture plots, with diversity and density held constant, are significantly changed when the arrangement (pattern) of individuals within that array is altered. However, mean yields of different mixture plots range from 2683.7 grams to 3701.9 grams. It is possible that with more replication significant differences may have been indicated. The proportional contributions of the separate species also remained unchanged. Also, it is possible that the life forms or physiological processes (i.e. rates of photosynthesis, nutrient uptake, proportions and absolute quantities of nutrients needed per unit of biomass produced, etc.) among the component species do not differ enough to give a gradient of combining ability among them. It should be noted that it is beyond the scope of this study to determine what, if any, are the physiological differences among the species used.

Competition Indices

In my diversity-yield experiment, the dominant component, Amaranthus, was suppressed most by intraspecific competition. Dominance is not necessarily directly related to competitive ability. Species in a community could be dominant and at the same time only be realizing a small proportion of their genetic potential for

productivity. Conversely, species could conceivably be realizing their full potential for productivity and still be a minor contributor to community NPP. In other words, if species A had a genetic potential to produce 100 grams, but only yielded 40 grams and species B could potentially produce 20 grams and, in fact, did yield 20 grams, then species A, as a producer, would be dominant to species B but at the same time, species B would be the better competitor. In order to more clearly demonstrate the intra- and interspecific relationships of the species in mixture plots, and to "equalize" the inherent weight differential among species, a competition index (CI) was developed (Table 5). The mean row weight of each species in pure stands was used as a base line to determine whether a species was affected (suppressed) more by intra- or interspecific competition. The CI is calculated by dividing this base-line mean row weight for each species, into mean row weights attained when those species grew between two rows of each of the other species. Consequently, the intraspecific CI is always one, by definition. Any situation in which the index is greater than one indicates that interspecific competitive stress, from that particular competitor, is less than stress from intraspecific competition. Conversely, any situation where the CI is less than one, indicates that interspecific competition stress is greater than that exerted through intraspecific competition. Amaranthus rows yielded more in mixture than in pure stands. Chenopodium produced more yield per row in mixture plots than in pure stands when it was in between rows of grasses. However, when Chenopodium was in mixture plots where it was between rows of Amaranthus, it yielded less per row than when in pure stands. Both Panicum and Setaria were more suppressed by

Table 5. Mean row weight of each species within the mixture plots.

Species within Mixture Plots	Mixture Plots				Relative Comp.** Ability Index (RCA)
	SACP	CAPS	RANDOM	PACS	PURE
<u>Amaranthus</u>					
Mean Row Weight	995.77	994.54	872.63	645.04	511.33
Competition Index*	1.95	1.95	1.71	1.26	1.00
					7.87
<u>Chenopodium</u>					
Mean Row Weight	452.48	344.65	387.16	398.74	396.04
Competition Index	1.14	0.87	0.98	1.01	1.00
					5.00
<u>Panicum</u>					
Mean Row Weight	239.04	240.70	159.20	121.15	347.76
Competition Index	0.69	0.69	0.46	0.35	1.00
					3.19
<u>Setaria</u>					
Mean Row Weight	113.53	271.05	170.81	177.06	296.03
Competition Index	0.38	0.92	0.58	0.60	1.00
					3.48

*Competition Index (CI) = $\frac{\text{Mean Row Weight of a Species in Pure Stand}}{\text{Mean Row Weight of the Species in a Treatment}}$

**Relative Competitive Ability Index = Sum of the CI's for that particular species

interspecific competition than by intraspecific competition.

Relative competitive abilities of each species in the mixture plots was determined by summing the competition indices of each species to give values that describe overall performance of each species. This value is the relative competitive ability index (RCA). A high index indicates a species is a good competitor. Based on their respective RCA's, the ranking of the component species, with regard to their competitive abilities, is Amaranthus > Chenopodium > Setaria > Panicum.

Amaranthus and Chenopodium were the best competitors of the four component species. Obviously these dominant species exhibited a greater rate of growth which is a function of many mechanisms (photosynthesis, root uptake rates, etc.). It is beyond the scope of this study to determine which mechanisms were most important in allowing Amaranthus and Chenopodium to be the dominants. Walter (1971) states that, "Where the growth cycles of individuals in a population are synchronous and light is nearly fully intercepted, victory goes to the individuals which achieve height quickest whether by producing (1) taller leaves (as in grasses), (2) longer petioles, (3) taller stems or (4) more perennial stems." All components were sown at the same time and germination was close to being synchronous. Chenopodium germinated about four to five days after the other species. It appeared that the competitive advantage was acquired by the two dicots by virtue of their fast growing vertical stems.

Experiment II - Pair-wise Competitive Ability Experiment

For experiment II, each species was subjected to intraspecific and interspecific competition. Results indicate that the dicots were superior competitors to the grasses, under conditions dictated by the experiment and that particular growing season. In a statistical sense, ranking the four species as to their competitive abilities was not possible since the effects of Amaranthus and Chenopodium on the target plants were not significantly different ($\alpha = 0.05$) and a clear trend was not apparent. The same is true for the grasses. About all that can be said statistically is that the dicots were significantly better competitors than the monocots; as was the case in the diversity-yield experiment.

Another way to look at the competitive abilities of the species used in this study is to calculate competition indices (CI) as was done in the diversity-yield experiment. Mean yields of target plants, when ringed by their own species, were used as base-line values. For each species, the mean yield of the target plants in each treatment was divided into the mean base-line yield to give the CI for each treatment. These values were then added to give a relative competitive ability (RCA) index for each species. Ranking was then accomplished, using the RCA for each species as the criterion. The greater the RCA, the higher the rank. Relative competitive abilities of the species were, from highest to lowest, Chenopodium > Amaranthus > Setaria > Panicum (Table 6). This is not the same sequence found with the relative competitive abilities of these species in the diversity-yield experiment (Table 5). It, therefore, does not support the suggestion of Watt (1964) concerning the predictability of pair-wise competitive ability experiments.

Table 6. Mean yields of target plants in grams when subjected to intra- and interspecific competition.

Target Plants	Competitors				RCA**
	Amaranthus	Chenopodium	Panicum	Setaria	
<u>Amaranthus</u>					
Mean weight	19.48	14.83	39.17	39.76	5.81
CI*	1.00	0.76	2.01	2.04	
<u>Chenopodium</u>					
Mean weight	11.18	10.90	66.06	53.33	12.97
CI	1.02	1.00	6.06	4.89	
<u>Panicum</u>					
Mean weight	3.72	5.52	17.03	23.71	2.92
CI	0.21	0.32	1.00	1.39	
<u>Setaria</u>					
Mean weight	6.87	6.13	15.11	12.99	3.15
CI	0.52	0.47	1.16	1.00	

Mean yield of target plants

*Competition Index = $\left(\frac{\text{when encircled by plants of its own species}}{\text{Mean yield of target plants for a particular treatment}} \right)$

**Relative Competitive Ability Index = (Sum of CI's for each species)

Control plant yields were not used as base line data since it appears environmental variables such as wind and heat may have suppressed their growth and resultant yield quite severely. Whether these variables affected control yields of the four species equally or differentially was not determined. However, it was evident that with Chenopodium and Panicum the yields of control plants were lower than they were in some treatments in which they were subjected to competition from other plants. Perhaps, even though the competitors were using the same resources from the same source as the target plant, their presence may have modified the physical microclimate (e.g. by providing a wind break, raising relative humidity, conserving heat at night, etc.) enough to make their presence more beneficial than harmful, in some instances. Undoubtedly, these species have evolved to grow in communities with neighboring plants. To put them in the open in a field, without neighboring plants, probably exposes them to conditions not conducive for optimal growth and reproduction. Harper (1964) followed this line of thought when he said, "It may be argued, therefore, that the essential qualities which determine the ecology of a species may only be detected by studying the reaction of its individuals to their neighbors and that the behavior of the individuals of the species in isolation may largely be irrelevant to understanding their behavior in the community."

Below Ground Biomass

Yield of below ground biomass in experiments I and II were estimated from random samples. Root weight values were lower than similar data from other studies on the same species in natural communities (Stephenson and Reed, personal communication). The lower

than expected root yields may have been partially due to watering the plots in the initial five weeks of the study. It has been shown that dry conditions are favorable to accumulation of organic matter below ground (Singh and Yadavah, 1974). Other investigators have shown that root/shoot ratios tend to increase with xeric conditions (Bray, 1963; Struik, 1965; Struik and Bray, 1970). Plants of the same species growing in drier habitats or in seasons of drought have a higher below ground dry matter production (Singh and Yadavah, 1974). Certainly watering the experimental site every three days for the first five weeks made the soil far more moist than in the surrounding natural communities. There is also a possibility that the sampling procedure may have been somewhat inadequate (especially for the fragile fibrous roots of the grasses), resulting in underestimation of the root weights. Data collected indicates that dicots suppressed root growth of neighboring plants more than the grasses did.

Root yield of each species was estimated for all competitive situations in both the diversity-yield experiment (Table 7) and the competitive ability experiment (Table 8). RCA indices, determined for roots of species in the diversity-yield experiment, indicated that ranking of competitive ability of roots was Amaranthus > Chenopodium > Setaria > Panicum. For the pair-wise competitive ability experiment, the ranking was Chenopodium > Amaranthus > Panicum > Setaria. The root yields of the dicots were suppressed less by competition than those of the grasses.

Table 7. Mean root yields in grams per row of each species when flanked by two rows of each of the mixture plot components, along with competition indices and competitive ability indices.

Species in Row	Competitors				RCA**
	Amaranthus	Chenopodium	Panicum	Setaria	Random
<u>Amaranthus</u>					
Mean weight	25.30	37.87	48.00	63.77	47.5
CI*	1.00	1.49	1.89	2.52	1.87
					8.77
<u>Chenopodium</u>					
Mean weight	13.41	41.06	51.73	32.55	20.11
CI	0.32	1.00	1.25	0.79	0.48
					3.84
<u>Panicum</u>					
Mean weight	1.86	3.90	13.96	8.37	3.81
CI	0.13	0.27	1.00	0.59	0.27
					2.26
<u>Setaria</u>					
Mean weight	1.28	3.93	2.50	5.19	5.43
CI	0.24	0.75	0.48	1.00	1.04
					3.51

*Competition Index (CI) = $\frac{\text{Mean row weight of a species in pure stand}}{\text{Mean row weight of the species in a treatment}}$

**Relative Competitive Ability Index_(x) = (Sum of all competition indices for species (X))

Table 8. Mean root yields of target plants for each species, along with corresponding competition indices and relative competitive ability indices.

Target Plant	Competitors			RCA**
	Amaranthus	Chenopodium	Panicum	Setaria
<u>Amaranthus</u>				
Mean weight	0.87	0.35	4.36	3.45
CI*	1.00	0.40	5.01	3.96
				10.37
<u>Chenopodium</u>				
Mean weight	0.60	0.58	7.05	3.87
CI	1.03	1.00	12.15	6.67
				20.85
<u>Setaria</u>				
Mean weight	0.28	0.21	0.47	0.38
CI	0.73	0.55	1.23	1.00
				3.51
<u>Panicum</u>				
Mean weight	0.15	0.23	0.42	0.96
CI	0.35	0.54	1.00	2.28
				4.17
*Competition Index = $\left(\frac{\text{Mean yield of target plant when encircled by plants of its own species}}{\text{Mean yield of target plants for a particular treatment}} \right)$				

**Relative Competitive Ability Index = (Sum of competition indices of a particular species)

CONCLUSIONS

The following points have come to light during the course of this study:

1. The diversity yield experiment demonstrated that mean yield of the highest yielding monoculture, Amaranthus, was comparatively higher than any of the mean yields of the mixture plots. However, it did not indicate that Amaranthus yields were significantly higher ($\alpha = 0.05$) than those of the mixtures. This could be possibly due to (1) lack of sufficient differential among the root growth patterns of the separate species, (2) use of a fixed density that disregards maximal yield densities of the separate species, and (3) insufficient replication.

2. Change of the arrangement of the pattern of the separate populations, within the mixtures, did not cause a significant difference in the yields of the mixtures. Once again, this could be due to lack of sufficient differential among the growth forms of the component species as well as the possibility of insufficient replication.

3. Distribution of the site biomass among the component species follows a geometric pattern similar to that which is predicted by the niche pre-emption hypothesis (Whittaker, 1965, 1969) for natural communities low in species richness and high in expression of species dominance.

4. Using yield as a criterion, dominance was clearly expressed in the diversity-yield plots. Amaranthus contributed greater than 50% of the yield in all the mixture plots.

5. The paired-species competitive ability experiment did not predict the relative performances of the four species when grown in mixture plots. It appears that this type of experiment does not allow one to rank a group of plants by their respective competitive abilities and consequently predict the outcome of different combinations.

6. In both the diversity yield experiment and the competitive ability experiment, the dicots were clearly superior to the monocots as competitors.

7. Root yields of the dicots were suppressed less by competition than those of the grasses.

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LITERATURE CITED

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APPENDICES

APPENDIX A-1

Analysis of variance table for comparison of treatment plot yields
in the diversity-yield experiment.

Source of Variation	df	SS	MS	F
Treatment	7	7272386.40	1038912.34	2.82*
Error	16	5888965.92	368060.37	
Total	23	13161352.32	572232.70	

APPENDIX A-1

Treatments								
	AMARAN.	ACPS	ASCP	CHENOP.	RANDOM	PANICUM	APCS	SETARIA
MEANS	4090.65	3701.90	3601.71	3168.31	3154.35	2691.13	2683.70	2368.25
2368.25	1722.40*	1333.65	1233.46	800.06	786.10	322.82	315.45	
2683.70	1406.55	1018.20	918.01	484.61	470.65	7.43		
2691.13	1399.52	1010.77	910.58	477.18	463.22			
3154.35	936.3	547.55	447.36	13.96				
3168.31	922.34	533.59	433.40					
3601.71	488.94	100.19						
3701.90	388.75							
4090.65								

Least significant range table for the Tukey w-procedure a posteriori test. The calculated LSR value is 1715.26.

APPENDIX A-2

Analysis of variance tables on competitive interactions within mixture plots. Criterion for treatment effect is the above ground yield by specific rows when bracketed by two other rows of competing plants.

AMARANTHUS:

Overall analysis of variance table:

Source of variance	df	SS	MS	F
Treatment	6	613.51	102.25	4.3**
Row	20	475.50	23.78	2.18**
Plants	506	5531.66	10.93	
Total	532	6620.79		

Sub-set Tables:

(Comparison of sub-set treatments - SAS, CAC, PAP, CAP)

Source of variance	df	SS	MS	F
Treatment	3	86.49	28.83	NS
Row	11	397.52	36.14	5.23***
Plants	247	1706.57	6.91	
Total	261	2190.58		

APPENDIX A-2

AMARANTHUS (Continued)

(Comparison of sub-set treatments - Random, AAA, SAC)

Source of variance	df	SS	MS	F
Treatment	2	14.17	7.09	NS
Row	9	77.99	8.67	NS
Plants	249	2522.34	10.13	
Total	260	2614.50		

(Comparison of sub-set treatments - CAP, RAN)

Source of variance	df	SS	MS	F
Treatment	1	10.94	10.94	NS
Row	7	138.13	19.73	2.79**
Plants	204	1445.21	7.08	
Total	212	1594.28		

(Comparison of sub-set treatments - SAS, Random)

Source of variance	df	SS	MS	F
Treatment	1	136.12	136.12	13.61*
Row	4	40.02	10.00	NS
Plants	157	2735.59	17.42	
Total	162	2911.73		

APPENDIX A-2

AMARANTHUS (Continued)

(Comparison of sub-set treatments - SAC, CAC)

Source of variance	df	SS	MS	F
Treatment	1	56.58	56.58	NS
Row	4	176.14	44.04	5.72***
Plants	103	793.46	7.70	
Total	108	1026.18		

(Comparison of sub-set treatments - SAC, SAS)

Source of variance	df	SS	MS	F
Treatment	1	162.04	162.04	14.04*
Row	4	46.16	11.54	NS
Plants	105	1472.70	14.03	
Total	110	1680.90	15.28	

APPENDIX A-2

CHENOPODIUM

Overall analysis of variance table:

Source of Variance	df	SS	MS	F
Treatment	6	214.81	35.8	5.73**
Row	17	106.20	6.25	NS
Plants	416	1865.37	4.48	
Total	439	2186.38		

Subset Tables:

(Comparison of sub-set treatments - PCP, SCS)

Source of Variance	df	SS	MS	F
Treatment	1	8.89	8.89	NS
Row	4	33.86	8.47	NS
Plants	96	497.55	5.18	
Total	101	540.30		

(Comparison of sub-set treatments - SCS, RANDOM, CCC)

Source of Variance	df	SS	MS	F
Treatment	2	29.43	14.72	NS
Row	9	50.01	5.56	NS
Plants	231	1264.40	5.47	
Total	242	1343.84		

APPENDIX A-2

CHENOPODIUM (continued)

(Comparison of sub-set treatments - PCP, RANDOM)

Source of Variance	df	SS	MS	F
Treatment	1	61.30	61.30	10.95*
Row	4	22.38	5.60	NS
Plants	134	921.42	6.88	
Total	139	1005.10		

(Comparison of sub-set treatments - RANDOM, CCC, ACS, ACP)

Source of Variance	df	SS	MS	F
Treatment	3	8.59	2.86	NS
Row	11	60.08	5.46	NS
Plants	273	1167.31	4.28	
Total	287	1235.98		

(Comparison of sub-set treatments - SCS, ACS)

Source of Variance	df	SS	MS	F
Treatment	1	30.12	30.12	8.83*
Row	4	13.63	3.41	MS
Plants	93	326.03	3.51	
Total	98	369.78		

APPENDIX A-2

CHENOPODIUM (continued)

(Comparison of sub-set treatments - CCC, ACS, ACP, ACA)

Source of Variance	df	SS	MS	F
Treatment	3	39.52	13.17	NS
Row	11	71.18	6.47	2.18*
Plants	233	692.89	2.97	
Total	247	803.59		

(Comparison of sub-set treatments - RANDOM, ACA)

Source of Variance	df	SS	MS	F
Treatment	1	44.97	44.97	13.38*
Row	4	13.44	3.36	NS
Plants	132	875.78	6.63	
Total	137	934.19		

APPENDIX A-2

PANICUM:

Overall analysis of variance table:

Source of Variance	df	SS	MS	F
Treatment	5	166.91	33.38	4.57*
Row	9	65.81	7.31	5.90***
Plants	298	368.15	1.24	
Total	312	600.87		

Sub-set Tables:

(Comparison of sub-set treatments - RANDOM, CPC)

Source of Variance	df	SS	MS	F
Treatment	1	0.43	0.43	NS
Row	4	42.83	10.71	NS
Plants	122	215.62	1.77	
Total	127	258.88		

(Comparison of sub-set treatments - SPS, PPP, APS, RANDOM)

Source of Variance	df	SS	MS	F
Treatment	3	152.46	50.82	NS
Row	8	56.42	7.05	4.9***
Plants	215	309.07	1.44	
Total	226	517.95		

APPENDIX A-2

PANICUM: (continued)

(Comparison of sub-set treatments - CPC, RANDOM, APA)

Source of Variance	df	SS	MS	F
Treatment	2	17.62	8.81	NS
Row	6	44.06	7.34	5.13***
Plants	162	232.22	1.43	
Total	170	293.90		

(Comparison of sub-set treatments - RANDOM, APA)

Source of Variance	df	SS	MS	F
Treatment	1	17.02	17.02	NS
Row	4	36.00	9.00	5.77***
Plants	122	189.74	1.56	
Total	127	242.76	1.90	

(Comparison of sub-set treatments - APS, APA)

Source of Variance	df	SS	MS	F
Treatment	1	31.34	31.34	11.96*
Row	4	10.49	2.62	4.76***
Plants	82	44.82	0.55	
Total	87	86.65		

APPENDIX A-2

PANICUM: (continued)

(Comparison of sub-set treatments - APS, CPC)

Source of Variance	df	SS	MS	F
Treatment	1	6.51	6.51	NS
Row	4	17.32	4.33	5.03***
Plants	82	70.70	0.86	
Total	87	94.53		

SETARIA:

Overall analysis of variance table:

Source of Variance	df	SS	MS	F
Treatment	4	111.54	27.89	18.35***
Row	10	17.83	1.78	NS
Plants	266	481.98	1.81	
Total	280	611.35		

APPENDIX A-2

SETARIA: (continued)

Sub-set Tables:

(Comparison of sub-set treatments - SSS, PSP)

Source of Variance	df	SS	MS	F
Treatment	1	9.60	9.60	NS
Row	4	5.04	1.26	NS
Plants	84	194.07	2.31	
Total	89	208.71		

(Comparison of sub-set treatments - RANDOM, CSC)

Source of Variance	df	SS	MS	F
Treatment	1	3.64	3.64	NS
Row	4	10.61	2.65	NS
Plants	142	271.70	1.85	
Total	147	285.95		

(Comparison of sub-set treatments - SSS, CSC)

Source of Variance	df	SS	MS	F
Treatment	1	45.91	45.91	26.69**
Row	4	6.89	1.72	NS
Plants	82	173.47	2.12	
Total	87	226.27		

APPENDIX A-2

SETARIA: (continued)

(Comparison of sub-set treatments - PSP, RANDOM)

Source of Variance	df	SS	MS	F
Treatment	1	6.01	6.01	NS
Row	4	8.76	2.19	NS
Plants	144	292.30	2.03	
Total	149	307.07		

(Comparison of sub-set treatments - SSS, RANDOM)

Source of Variance	df	SS	MS	F
Treatment	1	39.30	39.30	17.01*
Row	4	9.24	2.31	NS
Plants	148	322.29	2.18	
Total	153	370.83		

(Comparison of sub-set treatments - PSP, CSC)

Source of Variance	df	SS	MS	F
Treatment	1	13.22	13.22	8.26*
Row	4	6.41	1.60	NS
Plants	78	143.48	1.80	
Total	83	163.11		

APPENDIX A-2

SETARIA: (continued)

(Comparison of treatments - CSC, ASA)

Source of Variance	df	SS	MS	F
Treatment	1	8.58	8.58	NS
Row	4	6.31	1.58	NS
Plants	78	77.65	1.00	
Total	83	92.54		

(Comparison of treatments - RANDOM, ASA)

Source of Variance	df	SS	MS	F
Treatment	1	30.07	30.07	13.86*
Row	4	8.66	2.17	NS
Plants	144	226.47	1.57	
Total	149	265.20		

APPENDIX A-3

Analysis of variance tables on competitive interactions within mixture plots and their effect on root yields. Criterion for treatment effect is root yield by specific rows when bracketed by two other rows of competing plants.

SETARIA:

Overall analysis of variance table:

Source of Variance	df	SS	MS	F
Treatment	4	0.431	0.108	NS
Row	10	1.171	0.117	2.21***
Plants	107	5.631	0.053	
Total	121			

AMARANTHUS:

Overall analysis of variance table:

Source of Variance	df	SS	MS	F
Treatment	6	8.70	1.45	NS
Row	20	17.40	0.87	1.89*
Plants	58	26.84	0.46	
Total	84	50.80		

APPENDIX A-3

CHENOPODIUM:

Overall analysis of variance table:

Source of Variance	df	SS	MS	F
Treatment	6	5.98	1.00	3.57*
Row	16	4.53	0.28	NS
Plants	131	45.05	0.34	
Total	153	55.56		

Sub-set Tables:

(Comparison of sub-set treatments - PCP, SCS, CCC, RANDOM, ACP, ACS)

Source of Variance	df	SS	MS	F
Treatment	5	3.57	0.71	NS
Row	14	4.45	0.32	NS
Plants	121	43.40	0.36	
Total	140	51.42		

(Comparison of sub-set treatments - RANDOM, ACP, ACS, ACA)

Source of Variance	df	SS	MS	F
Treatment	3	1.66	0.55	NS
Row	7	1.56	0.22	NS
Plants	89	27.03	0.30	
Total	99	30.25		

APPENDIX A-3

CHENOPODIUM: (continued)

(Comparison of sub-set treatments - PCP, ACA)

Source of Variance	df	SS	MS	F
Treatment	1	4.41	4.41	13.36*
Row	4	1.31	0.33	NS
Plants	26	10.31	0.40	
Total	31	16.03		

(Comparison of sub-set treatments - ACA, CCC)

Source of Variance	df	SS	MS	F
Treatment	1	1.86	1.86	13.29*
Row	7	0.98	0.14	NS
Plants	21	5.24	0.25	
Total	29	8.08		

APPENDIX A-3

PANICUM:

Overall analysis of variance table:

Source of Variance	df	SS	MS	F
Treatment	5	6.89	1.38	13.8*
Row	12	1.22	0.10	2.0*
Plants	167	7.56	0.05	
Total	184	15.67		

Sub-set Tables:

(Comparison of sub-set treatments - PPP, SPS, APS)

Source of Variance	df	SS	MS	F
Treatment	2	0.58	0.29	NS
Row	6	0.91	0.15	3.79**
Plants	91	3.60	0.04	
Total	99	5.09		

(Comparison of sub-set treatments - APS, CPC, RANDOM, APA)

Source of Variance	df	SS	MS	F
Treatment	3	0.75	0.25	NS
Row	9	0.63	0.07	NS
Plants	105	4.76	0.05	
Total	117	6.14		

APPENDIX A-3

PANICUM: (continued)

(Comparison of sub-set treatments - PPP, CPC)

Source of Variance	df	SS	MS	F
Treatment	1	1.14	1.14	12.67*
Row	4	0.37	0.09	NS
Plants	42	2.72	0.06	
Total	47	4.23		

(Comparison of sub-set treatments - APA, SPS)

Source of Variance	df	SS	MS	F
Treatment	1	2.03	2.03	33.83**
Row	4	0.23	0.06	NS
Plants	60	2.00	0.03	
Total	65	4.26		

APPENDIX A-4

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on shoot yields:

Amaranthus target plants - ANOVA table:

Source of variance	df	SS	MS	F
Among	4	88.85	22.21	3.6
Within	39	240.57	6.17	
Total	43	329.42	7.66	

Amaranthus target plants - least significant range table:

		<u>Chenopodium</u>	<u>Amaranthus</u>	<u>Panicum</u>	<u>Setaria</u>	<u>Control</u>
		3.38	3.66	5.45	5.99	7.52
Control	7.52	4.14*	3.86*	2.07	1.53	
<u>Setaria</u>	5.99	5.99*	2.33	0.54		
<u>Panicum</u>	5.45	5.45*	1.79			
<u>Amaranthus</u>	3.66	0.28				
<u>Chenopodium</u>						

LSR value - 3.34, $\alpha = 0.05$

APPENDIX A-4

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on shoot yields of Chenopodium album.

Analysis of variance table:

Source of Variation	df	SS	MS	F
Among	4	158.61	39.65	10.39***
Within	59	225.32	3.82	
Total	63	383.93	6.09	

Least significant range table:

	<u>Amaranthus</u>	<u>Chenopodium</u>	Control	<u>Setaria</u>	<u>Panicum</u>
	3.19	3.28	6.06	7.09	7.61
<u>Panicum</u>	7.61	4.42*	4.33*	1.55	0.52
<u>Setaria</u>	7.09	3.90*	3.81*	1.03	
Control	6.06	2.87*	2.78*		
<u>Chenopodium</u>	3.28	0.09			
<u>Amaranthus</u>	3.19				

LSR value = 2.16, α = 0.05

APPENDIX A-4

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on Panicum capillare shoot yields.

Analysis of variance table:

Source of variation	df	SS	MS	F
Among	4	78.43	19.61	12.80***
Within	55	84.29	1.53	
Total	59	162.73	2.67	

Least significant range table:

	<u>Amaranthus</u>	<u>Chenopodium</u>	<u>Panicum</u>	<u>Setaria</u>	Control
	1.84	2.24	4.00	4.33	4.66
Control	4.66	2.82*	2.42*	0.66	0.33
<u>Setaria</u>	4.33	2.49*	2.09*	0.33	
<u>Panicum</u>	4.00	2.16*	1.76*		
<u>Chenopodium</u>	2.24	0.08			
<u>Amaranthus</u>	1.84				

LSR value = 1.42, α = 0.05

APPENDIX A-4

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on Setaria viridis shoot yields.

Analysis of variance table:

Source of variation	df	SS	MS	F
Among	4	25.48	6.37	7.48***
Within	46	39.72	0.86	
Total	50	65.20	1.30	

Least significant range table:

		<u>Chenopodium</u>	<u>Amaranthus</u>	<u>Setaria</u>	<u>Panicum</u>	Control
		2.32	2.39	3.50	3.82	4.11
Control	4.11	1.79*	1.72*	0.61	0.29	
<u>Panicum</u>	3.82	1.50*	1.43*	0.32		
<u>Setaria</u>	3.50	1.18*	1.11			
<u>Amaranthus</u>	2.39	0.07				
<u>Chenopodium</u>	2.32					

LSR value = 1.15, α = 0.05

APPENDIX A-5

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on root yields of Amaranthus retroflexus.

Analysis of variance table:

Source of variation	df	SS	MS	F
Among	4	2.92	0.73	1.62
Within	15	6.80	0.45	
Total	19	9.72	0.51	

Least significant range table:

		<u>Amaranthus</u>	<u>Chenopodium</u>	<u>Control</u>	<u>Setaria</u>	<u>Panicum</u>
		0.89	1.12	1.61	1.76	1.87
<u>Panicum</u>	1.86	0.97	0.74	0.25	0.10	
<u>Setaria</u>	1.76	0.87	0.64	0.15		
<u>Control</u>	1.61	0.72	0.49			
<u>Chenopodium</u>	1.12	0.23				
<u>Amaranthus</u>	0.89					

LSR value = 1.47, α = 0.05

APPENDIX A-5

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on root yields of Chenopodium album.

Analysis of variance table:

Source of variation	df	SS	MS	F
Among	4	7.32	1.83	6.31***
Within	20	5.85	0.29	
Total	24	13.17	0.54	

Least significant range table:

		<u>Amaranthus</u>	<u>Chenopodium</u>	Control	<u>Setaria</u>	<u>Panicum</u>
		0.74	0.75	1.67	1.87	2.51
<u>Panicum</u>	2.51	1.77*	1.76*	0.84	0.64	
<u>Setaria</u>	1.87	1.13*	1.12*	0.20		
Control	1.67	0.93	0.92			
<u>Chenopodium</u>	0.75	0.75				
<u>Amaranthus</u>	0.74					

LSR value = 1.02, $\alpha = 0.05$

APPENDIX A-5

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on root yields of Panicum capillare.

Analysis of variance table:

Source of Variation	df	SS	MS	F
Among	4	1.74	0.43	7.16***
Within	46	2.76	0.06	
Total	50	4.50	0.09	

Least significant range table:

	<u>Amaranthus</u>	<u>Chenopodium</u>	<u>Panicum</u>	Control	<u>Setaria</u>
	0.35	0.47	0.62	0.78	0.86
<u>Setaria</u>	0.86	0.51*	0.39*	0.24	0.08
Control	0.78	0.43*	0.31*	0.16	
<u>Panicum</u>	0.62	0.27	0.15		
<u>Chenopodium</u>	0.47	0.12			
<u>Amaranthus</u>	0.35				

LSR value = 0.31, α = 0.05

APPENDIX A-5

Analysis of variance and least significant range tables for the competitive ability experiment to measure the effect of competitive interactions on root yields of Setaria viridis.

Analysis of variance table:

Source of Variation	df	SS	MS	F
Among	4	0.26	0.07	2.83*
Within	29	0.69	0.02	
Total	33	0.95	0.03	

Least significant range table:

		<u>Chenopodium</u>	<u>Amaranthus</u>	<u>Setaria</u>	Control	<u>Panicum</u>
		0.44	0.52	0.58	0.65	0.68
<u>Panicum</u>	0.68	0.24*	0.16	0.10	0.03	
Control	0.65	0.21	0.13	0.07		
<u>Setaria</u>	0.58	0.14	0.06			
<u>Amaranthus</u>	0.52	0.08				
<u>Chenopodium</u>	0.44					

LSR value = 0.22, α = 0.05

APPENDIX A-6

Calculations of Chi-square values to determine goodness of fit of experimental data with data estimated to fit a geometric progression series.

Mixture (RANDOM)

Species rank	Observed % yield of total yield	Estimated % yield of total yield
1	25	27.50
2	11	13.75
3	9	6.87

$$\chi^2 = \frac{(25-27.5)^2}{27.5} + \frac{(11-13.75)^2}{13.75} + \frac{(9-6.87)^2}{6.87}$$

$$\chi^2 = 1.44 \text{ (NS)}$$

Mixture (CAPS)

Species rank	Observed % yield of total yield	Estimated % yield of total yield
1	18	27.00
2	15	13.50
3	13	6.75

$$\chi^2 = \frac{(18-27)^2}{27} + \frac{(15-13.5)^2}{13.5} + \frac{(13-6.75)^2}{6.75}$$

$$\chi^2 = 8.96^*$$

*These Chi-square values were tested for significance using two degrees of freedom and an α value of 0.05.

APPENDIX A-6

Calculations of Chi-square values to determine goodness of fit of experimental data with data estimated to fit a geometric progression series.

Mixture (SACP)

Species rank	Observed % yield of total yield	Estimated % yield of total yield
1	25	28
2	13	14
3	6	7

$$\chi^2 = \frac{(25-28)^2}{28} + \frac{(13-14)^2}{14} + \frac{(6-7)^2}{7}$$

$$\chi^2 = 0.53 \text{ (NS)*}$$

Mixture (PACS)

Species rank	Observed % yield of total yield	Estimated % yield of total yield
1	33	26.50
2	14	13.25
3	10	6.62

$$\chi^2 = \frac{(33-26.5)^2}{26.5} + \frac{(14-13.25)^2}{13.25} + \frac{(10-6.62)^2}{6.62}$$

$$\chi^2 = 3.36 \text{ (NS)*}$$

*These Chi-square values are not significant, at the $\alpha = 0.05$ level using two degrees of freedom.

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