Oecologia (Berl.) 45, 366–371 (1980)

Oecologia

Effects of Diversity and Pattern on Relative Yields of Four Michigan First Year Fallow Field Plant Species

Glenn C. Kroh* and Stephen N. Stephenson[1]

[1] Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48823, USA

Summary. 1. A study was designed to investigate the effects of intra and inter-specific competition on the productivity of single and multi-species stands of plants normally dominant in first year old-field communities of mid-Michigan. The four species used were *Amaranthus retroflexus, Chenopodium album, Panicum capillare,* and *Setaria viridis.*

2. Specifically, we tested (1) the relationship between diversity and productivity, (2) the effect of arrangement (pattern) of individuals within an array of old-field dominants on yield and (3) the expression of dominance and resultant allocation of yields within mixture arrays of different plant species. In direct contrast to many earlier studies, our experiments were completed in the field under natural conditions.

3. Mean yield of the highest yielding monoculture, *Amaranthus,* was greater than any of the yields of the mixture plots.

4. Changing the pattern within mixtures had no significant effect on the yields of the mixture plots. Distribution of biomass among the component species followed a geometric pattern similar to that predicted by the niche pre-emption hypothesis (Whittaker, 1965, 1969). Using yield as a criterion, dominance was clearly expressed in the mixture plots. *Amaranthus* contributed more than 50% of the yield in all of the mixture plots.

5. A relative competitive ability index (RCA) was developed to demonstrate more clearly the intra and interspecific relationships among the species in mixture plots and to "equalize" the inherent weight differential among species. Relative Competitive Ability, from highest to lowest, was *Amaranthus, Chenopodium, Setaria* and *Panicum.*

6. The paired species experiment demonstrated that the performance of species in multi-species arrays cannot be predicted from paired competition experiments.

7. In the diversity-yield experiment and the paired-species competitive ability experiment, dicotyledons were clearly superior to monocotyledons.

Introduction

The purpose of our study was to determine the effect of competition on the yield of pure and mixture stands of species normally dominant in first year old-field communities of mid-Michigan. More specifically, we investigated: (1) the relationship between productivity and diversity in a given system, (2) effect of arrangement (pattern) alteration of individuals within a given plant array, on the yield of that array, and (3) the expression of dominance and resultant allocation of yields within mixture arrays of different plant species.

Shoots of these annual plants exhibit a flexible growth response to interference from neighboring plants. Biennials and perennials, characteristic of later successional stages, were not used because they are prone to vegetative reproduction (by rhizomes and stolons) and it is impossible to clearly define an individual.

The term competition in this paper is used in the manner that *Harper* (1960) 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.

Present address: *Department of Biology, Texas Christian University, Fort Worth, Texas 76129, U.S.A.

Materials and Methods

Two experiments were conducted with two dicotyledonous plants, *Amaranthus retroflexus* and *Chenopodium album,* and two monocotyledonous plants, *Panicum capillare* and *Setaria viridis.* These species are representative of typical plant forms in the first year fallow field community. In experiment I, mixture plots containing four species and pure stands of each species were grown. Using a randomized block experimental design, yields of mixture plots and pure stands were compared and analyzed statistically by one-way analysis of variance. In each block, four plots were monocultures and four were mixtures. Each mixture had an equal number of plants of each species but was planted in a different pattern (Fig. 1). All plots had the same density, allowing a valid comparison of the high diversity (mixture) plots with low diversity (monoculture) plots. In addition, by shifting location of rows of different species in the mixture plots, we could determine the effect of altered interspecific competition in plots with the same species diversity and density. Each plot contained 128 plants arranged in eight rows of sixteen plants each. Inter-plant distance was 15 cm, giving an effective density of 51 plants m^{-2}, which approximated that found in the natural state.

A cultivated field, previously planted with soybean, was plowed, tilled and harrowed. Black polyethylene sheets with a 128 hole pattern were used as planting templates, and were left in position. Several seeds were sown per template hole, but after germination plants were thinned to one per hole. If no seeds germinated, seedlings were transplanted to the template holes from reservoir plots. *Chenopodium* had a germination rate of only 25% and reservoir plots were exhausted, so seedlings from the natural

0029-8549/80/0045/0366/$01.20

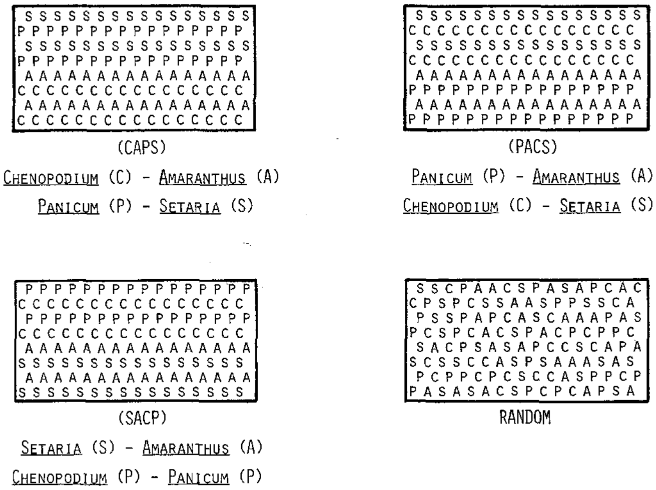

Fig. 1. The four basic patterns of plants in the mixture plots

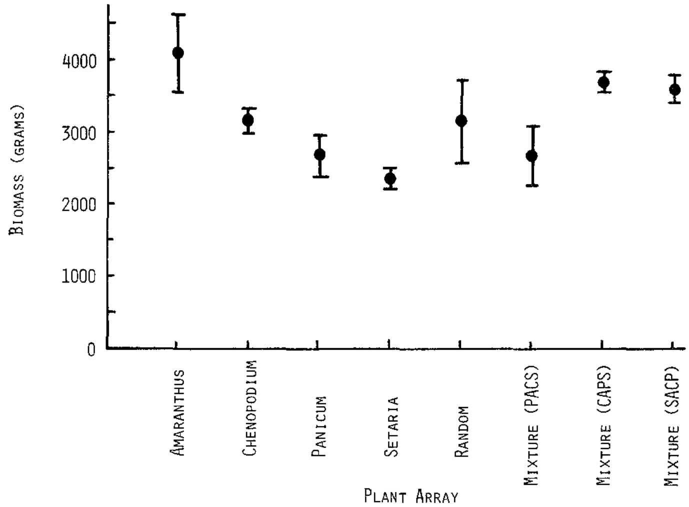

Fig. 2. Total above ground biomass per plot in the diversity-yield experiment. Letters in parentheses indicate species spacing in that particular plot. (PACS), for example indicates that *Panicum* and *Amaranthus* are side by side and *Chenopodium* and *Setaria* are side by side. Vertical bars represent ± one standard error of the mean

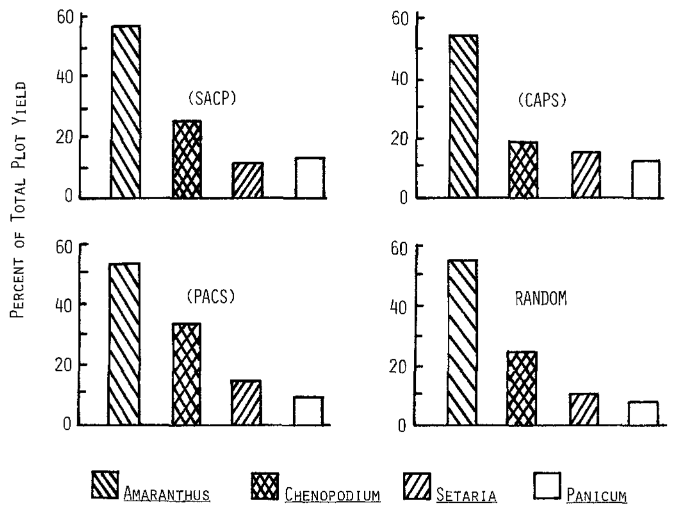

Fig. 3. Relative contributions to total plot yield by component species of mixture plots in the diversity-yield experiment. Plant arrays, in parentheses, are described in Fig. 1

population, adjacent to the experimental plots, were used. All plots were watered equally for the first five weeks. At the end of five weeks, watering was terminated and the polyethylene templates were removed.

In mid-September all plots were harvested. Individual rows of plants were put into coded plastic bags and stored at 5° C. Within each row, 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 h, and the weights were recorded.

Total plot yields and yield per species in each treatment were analyzed by a one-way analysis of variance. Within plot analysis determined overall average yield per plant of each species in each treatment. The resulting yields were compared using a one-way analysis of variance.

Experiment II was designed to compare species in all possible pairs. 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 used by Goodall (1960), Harper (1961) and Sakai (1965) in similar experiments. Control plants were sown singly, without a ring of competitors.

Effects of intra and interspecific competition were determined by comparing standing crop (dry weight) of target plants in different treatments by a one-way analysis of variance and 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. The plants were dried and weighed as in experiment I.

Results

Experiment I. The Diversity-Yield Plots

After germination, the dicots, *Amaranthus* and *Chenopodium*, appeared to be the fastest growing plants in the mixture plots. By the first week, *Amaranthus* was dominant in the mixture plots, and *Chenopodium* was the second most productive. The crown of *Chenopodium* was nearly cylindrical: that of *Amaranthus* was conical but wider at the base. *Amaranthus* had a dominant central tap root whereas *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 coarser than those of *Panicum*.

Mean total shoot yield per plot ranged from a high of 4090.65 grams in pure stands of *Amaranthus* to a low of 2368.25 grams in *Setaria* monocultures (Fig. 2). Analysis of variance indicated a significant difference between these treatments ($P=0.05$). Although yields of monocultures of *Amaranthus* were consistently greater than those of the other treatments also, the differences were not significant ($P=0.05$). Ranking of yield per species in pure stands was, from highest to lowest, *Amaranthus*, *Chenopodium*, *Panicum* and *Setaria*.

Relative contributions to mixture plot yield by the component species exhibit definite and repeatable trends. The hierarchy of

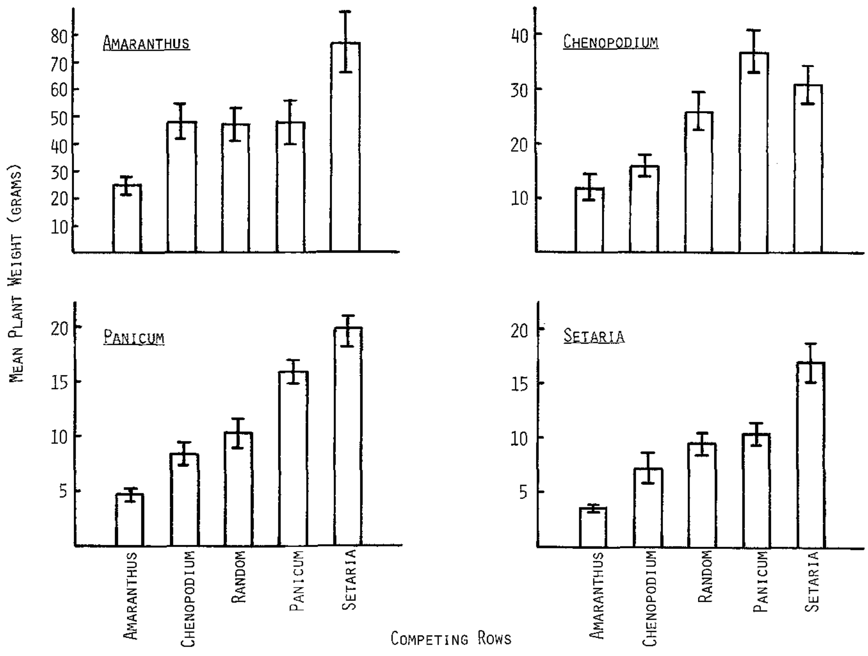

Fig. 4. Mean yield per plant located between two rows of the mixture plot component species. Vertical bars represent ± one standard error of the mean

Table 1. Average root weight per plant of each species when under competitive stress from adjacent rows

Competitor (flanking) Rows	Root weight							
	Amaranthus		*Chenopodium*		*Panicum*		*Setaria*	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Amaranthus	2.36	0.52	0.70	0.21	0.19	0.03	0.10	0.03
Chenopodium	5.22	1.07	1.55	0.66	0.29	0.05	0.26	0.05
Random	1.98	0.51	1.65	0.23	0.27	0.05	0.32	0.05
Panicum	2.33	0.71	2.79	0.55	0.68	0.07	0.28	0.05
Setaria	8.18	1.98	2.20	0.45	0.61	0.06	0.49	0.13

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 did *Setaria* (Fig. 3).

Within the plots, *Amaranthus* yielded more in mixture than in pure stands. *Chenopodium* yielded more in mixture plots than in pure stands when it was between rows of grasses. However, when *Chenopodium* was planted in mixture plots between rows of *Amaranthus*, it yielded less than in pure stands. Both *Panicum* and *Setaria* were more suppressed by interspecific competition than by intraspecific competition. *Amaranthus* appeared to be the best competitor and *Setaria* the poorest (Fig. 4). Lowest shoot yields occurred when the species were between two rows of *Amaranthus*. Significantly higher shoot yields were attained when they were flanked by grasses. *Chenopodium* had a significantly greater effect than *Panicum* on depressing shoot yields of all species except *Amaranthus*. There was little difference between effects of *Panicum* or *Chenopodium* on the mean yield of *Amaranthus*. Mean root yields of species within plots, except for *Amaranthus* were significantly lower when subjected to competition from the dicots than from the grasses (Table 1).

Table 2. Mean shoot and root weights of target plants in experiment II

Target plant	Competitor	Shoot weight		Root weight	
		Mean	SE	Mean	SE
Amaranthus	Amaranthus	19.49	10.14	0.87	0.28
	Chenopodium	14.83	4.88	1.56	0.71
	Panicum	39.18	11.99	4.36	1.50
	Setaria	39.76	8.49	3.45	1.31
	Control	58.77	10.72	2.78	0.72
Chenopodium	Amaranthus	11.18	2.09	0.60	0.18
	Chenopodium	10.9	0.94	0.58	0.06
	Panicum	66.07	16.86	7.05	4.25
	Setaria	53.34	10.31	3.87	1.72
	Control	40.28	4.62	3.10	0.37
Panicum	Amaranthus	3.72	0.64	0.15	0.04
	Chenopodium	5.53	1.38	0.23	0.03
	Panicum	17.05	2.35	0.42	0.06
	Setaria	23.71	6.90	0.96	0.41
	Control	21.81	2.41	0.66	0.10
Setaria	Amaranthus	6.88	1.82	0.28	0.05
	Chenopodium	6.13	1.65	0.21	0.04
	Panicum	15.11	1.78	0.47	0.07
	Setaria	12.99	1.57	0.39	0.10
	Control	17.65	2.28	0.44	0.08

Experiment II. Competitive Ability

In all cases, the dicots, *Chenopodium* and *Amaranthus*, were the most effective competitors (Table 2). Target plants of all species attained lowest shoot and root yields when surrounded by either of the dicots. Root yields of target plants surrounded by either of the dicots were not significantly different. Similarly, the effects of the competitor rings of either *Panicum* or *Setaria* on root yields of all species were not significantly different.

Discussion

Diversity and Yield

One primary objective of this study was to determine whether a mixture of different naturally co-occurring plant species produces a greater biomass than do pure stands of the component species of the mixture. Plant species used in this study normally coexist in natural plant communities. Our experiments were made under natural field conditions, in contrast to the glasshouse experiments of Bornkamm (1961) and Haizel (1972). Mixture yields concur with their results, as they were less than the highest yielding monoculture (*Amaranthus*) but greater than the lowest monoculture yield (*Setaria*). Growth forms of plant species used in this study may not be sufficiently different to allow them to exploit resources in significantly different ways. Whittington and O'Brien (1968) concluded 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. Even though the root growth patterns of the dicots and monocots differed, they still penetrated to the same depth and presumably acquired soil nutrients in the same area. In this respect, biennial or perennial species, representative of later successional stages might have produced different results because they exhibit root systems that range from fibrous sub-surface roots in some grasses to deeply penetrating tap roots.

Another aspect to consider with regard to the lower yields of mixture plots was 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 used as a base density of each species in mixture plots. In this way, mixture plots could be designed that would exhibit minimal intraspecific competition stress. In addition, utilization of species with different growth patterns would also enhance the "combining ability" of the species through minimizing interspecific competition.

Allocation of Biomass Among Species in the Mixture Plots

A good measure of how several species utilize available resources is how the resultant yield is allocated among them. 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) predicts that the distribution will approach a geometric series in communities where dominance is strongly developed and the number of species is small.

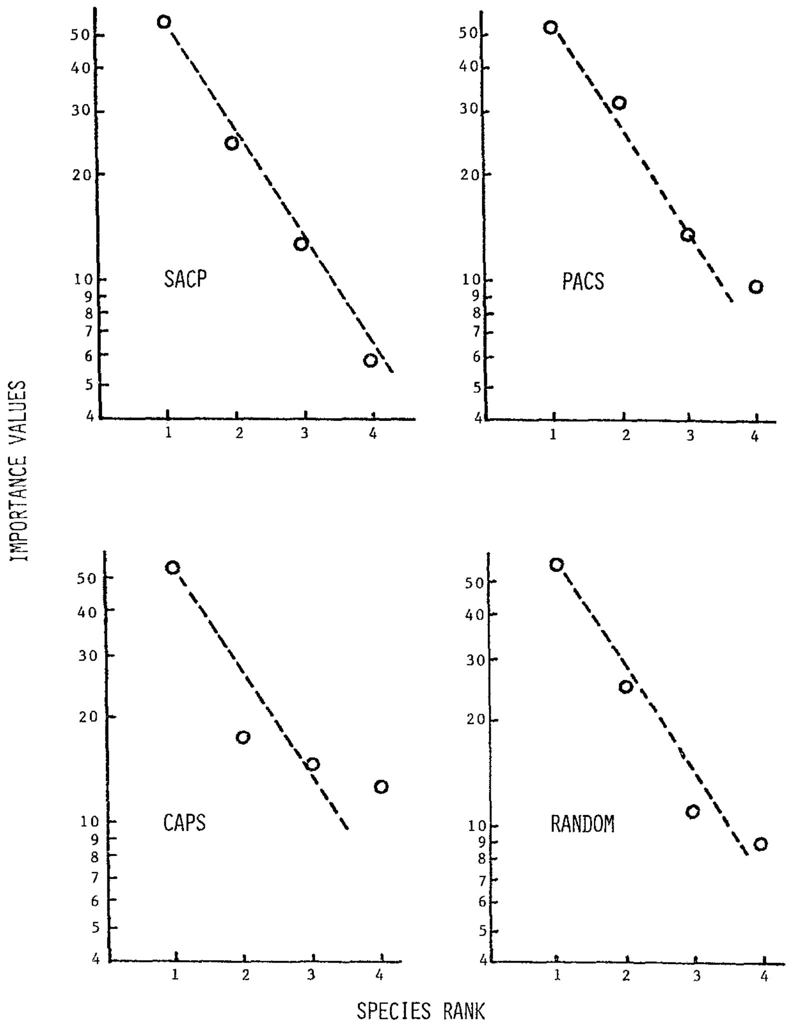

Fig. 5. Distribution of importance values of the component species of mixture plots. The dotted lines (----) represent the predicted geometric series curve for each plot, using the highest species importance value as the initial point. Species arrays noted in capital letters are described in Fig. 1

Table 3. Importance value of each species within the mixture plots

Mixture plot	Species			
	Amaranthus	Chenopodium	Panicum	Setaria
Setaria-Amaranthus Chenopodium-Panicum	56	25	13	6
Chenopodium-Amaranthus Panicum-Setaria	54	18	13	15
Panicum-Amaranthus Chenopodium-Setaria	53	33	10	14
Random	55	25	9	11
	54.5	25.25	11.25	11.5

Importance value = (Species Yield per Plot/Total Yield per Plot) × 100

Since densities and frequencies of species in experiment I were equal, the relative importance values among the species are equal to their relative yields. Distribution of their yields generally followed a geometric series pattern (Fig. 5), indicating a strong expression of dominance within the arrays. Distributions were compared to that predicted by a geometric series with a Chi-square test ($P = 0.05$). In all mixture plots except (CAPS), the distribution of total yield among the species did not differ significantly from that predicted by a geometric series curve (Fig. 5). In the (CAPS) plots, *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* yielded about 55% of the total biomass, based on dry weight yield. *Chenopodium* 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 3).

It is interesting that the geometric series curve describes the allocation of site resources among the species in experiment I as well as among species in a natural old-field community (Stephenson, 1973). However, Stephenson found that *Panicum* and *Setaria* in the field were both more productive than *Chenopodium*, in contrast to the findings of the present study. 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 and allowed it to attain a greater than normal importance.

Another experimental constraint, the synchronous germination of the component species, coincidentally paralleled that of the natural fallow-field community on the periphery of the experimental plot. Staggered sowing of the component species might have altered 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.

Pattern and Yield

Results of experiment I indicate that the net primary productivities of the mixture plots, with constant diversity and density, are not significantly changed when the arrangement (pattern) of individuals within that array is altered. Even though mean yields of different mixture plots ranged from 2683.7 grams to 3701.9 grams, the proportional contributions of the separate species remained unchanged. 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 may not differ enough to give a definite gradient of combining ability among them.

Table 4. Mean plant weight of each species within the mixture plots

Species Within Mixture Plots	Mixture plots					RCA[b]
	SACP	CAPS	RAND	PACS	PURE	
Amaranthus						
Mean Plant Weight	54.55	56.75	46.1	40.89	30.99	
Competition Index[a]	1.75	1.83	1.49	1.32	1.00	7.39
Chenopodium						
Mean Plant Weight	27.38	21.60	26.11	24.19	23.89	
Competition Index	1.15	0.90	1.09	1.01	1.00	5.15
Panicum						
Mean Plant Weight	14.48	15.86	10.35	7.97	22.18	
Competition Index	0.65	0.72	0.47	0.36	1.00	3.20
Setaria						
Mean Plant Weight	7.42	17.67	9.58	11.8	19.51	
Competition Index	0.38	0.91	0.49	0.60	1.00	3.38

[a] Competition Index

$= \frac{\text{Mean Plant Weight of the Species in a Treatment}}{\text{Mean Plant Weight of the Species in Pure Stand}}$

[b] Relative Competitive Ability Index

= Sum of the Competition Index for that Particular Species

Competition Indices

In experiment I, the dominant species, *Amaranthus*, was the one most depressed by intraspecific competition. Dominance is not necessarily directly related to competitive ability. A species in a community could be dominant and at the same time only be realizing a small proportion of its genetic potential for productivity. Conversely, a species could conceivably be realizing its full potential for productivity and still be a minor contributor to community production.

In order to demonstrate more clearly 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 4). The CI is calculated by dividing the mean plant weight of each species in pure stands by the mean plant weight of the species in each of the mixture treatments. By definition, the intraspecific CI is always one. If CI is greater than one, interspecific competitive stress is less than stress from intraspecific competition, and conversely if CI is less than one.

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 is *Amaranthus* > *Chenopodium* > *Setaria* > *Panicum*.

Table 5. Mean yield of target plants when subjected to intra- and interspecific competition

Target Plants	Competitors				RCA[b]
	Amaranthus	Chenopodium	Panicum	Setaria	
Amaranthus					
Mean Weight	19.48	14.83	39.17	39.76	
CI[a]	1.00	0.76	2.01	2.04	5.81
Chenopodium					
Mean Weight	11.18	10.90	66.06	53.33	
CI	1.02	1.00	6.06	4.89	12.97
Panicum					
Mean Weight	3.72	5.52	17.03	23.71	
CI	0.21	0.32	1.00	1.39	2.92
Setaria					
Mean Weight	6.87	6.13	15.11	12.99	
CI	0.52	0.47	1.16	1.00	3.15

[a] Competition Index

$$= \frac{\text{(Mean yield of target plant for a particular treatment)}}{\text{Mean yield of target plant}}$$

When encircled by plants of its own species

[b] Relative Competitive Ability Index

=(Sum of CI's for each species)

Pair-Wise Competitive Ability

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.

The competitive abilities of the species were compared by competition indices (CI) as was done in the diversity-yield experiment. The mean yield of target plant, when ringed by others of the same species, was used as the numerator. Relative competitive abilities of the species were, from highest to lowest, *Chenopodium, Amaranthus, Setaria, Panicum* (Table 5). This is not the same sequence found with the relative competitive abilities of these species in the diversity-yield experiment (Table 4).

Control plant yields were not used as base-line data since it appears environmental variables such as wind and heat, as indicated by descication, 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 the yields of control plants of *Chenopodium* and *Panicum* were lower than in some treatments in which they were subjected to competition from other plants. 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. 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." The comparative results of experiments I and II which predicted different rankings of relative competitive abilities, support the above hypothesis.

References

Bornkamm, R.: Competition for light in arable plants (German text). Flora Jene **151**, 126–143 (1961)

Goodall, D.W.: Quantitative effects of intraspecific competition: An experiment with mangolds. Bull. Res. Coun. of Israel Sec. D. Botany **8**, 181–194 (1960)

Haizel, K.A.: The productivity of mixtures of two and three species. J. Appl. Ecol. **9**, 601–608 (1972)

Harper, J.L.: Approaches to the study of plant competition. *Mechanisms in Biological Competition* (F.L. Milthorpe ed.), pp. 1–39. London: Oxford Univ. Press (1961)

Harper, J.L.: The individual in the population. J. Ecol. (Suppl.) **52**, 149–158 (1964)

Sakai, K.: Competition in plants and its relation to selection. Cold Spring Harbor Symp. Quant. Biol. **20**, 137–157 (1955)

Stephenson, S.N.: A comparison of productivity and diversity in early and late season old-field communities. Mich. Acad. **5 (3)**, 325–334 (1973)

Whittaker, R.H.: Dominance and diversity in land plant communities. Science **147**, 250–260 (1965)

Whittaker, R.H.: "Evolution of diversity in plant communities." Diversity and Stability in Ecological Systems, Brookhaven Symposia in Biology **22**, 178–260 (1969)

Whittaker, R.H.: (1970). Communities and Ecosystems. pp 162. Macmillan, London

Whittington, W.J., O'Brian, T.A.: A comparison of yields from plots sown with a single species or a mixture of grass species. J. Appl. Ecol. **5**, 209–213 (1968)

Received December 10, 1979