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Performance and Stability of Mixtures of Grain Sorghum

I. Relationship Between Level of Genetic Diversity and Performance

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Summary. In the absence of intergenotypic interactions the expected yield of randomly constituted, equiproportional mixtures of genotypes is shown to be independent of the number of components. However, with positive, additive interactions, the expected yield of a mixture is expected to be a monotonically increasing function of the number of components. The observed relationship between level of genetic diversity and mean yield, seed number and seed size for mixtures of inbred lines of grain sorghum closely followed the relationships expected under the assumption of additive interaction effects. However, estimates of the first and higher order components of the total interaction effect among the sorghum lines indicated that higher order interaction effects were often as great or greater than their first order counterparts, and opposite in sign, and that they may thus have had a cancelling effect in mixtures containing three or more components. These findings are discussed in terms of the relationship between level of genetic diversity and performance, and in connection with problems associated with the development of commercial multiline varieties.

Introduction

In recent years considerable research effort has been devoted to comparative studies of the relative performance of genetically heterogeneous and homogeneous populations in a wide range of crop plants (reviews in Jensen, 1952; Simmonds, 1962 and Allard, 1967). These studies suggest that, in some circumstances, intrapopulational variability may result in: i. increased yields through more efficient use of environmental resources (Gustafsson, 1953; Jensen, 1965); ii. greater stability of performance in diverse environments (Probst, 1957; Allard, 1961) and iii. a reduction in disease and insect damage (Suneson, 1960; Leonard, 1969). In the light of these findings a number of authors have suggested that it may be possible to utilise intra-varietal genetic diversity in commercial varieties more effectively than it has been in the past.

However, despite the extensive research that has been done, a number of basic questions remain unanswered. These include: 1. What is the relationship between level of genetic diversity, yield, and stability of yield? 2. What factors determine the optimum level of variability to incorporate into a commercial variety? 3. What is the optimal population structure of a heterogeneous cultivar (e.g., reconstitutable mixture, bulk hybrid population)? 4. Does this optimum vary with species and environment? The aims of the present study, which is part of a series of studies of various aspects of the relationship between population structure and performance (Allard and Adams, 1968, 1969; Clay and Allard 1969; Sammeta and Allard, in preparation), were to describe the effects of increasing levels of genetic diversity within a population on its performance and stability of performance in terms of theoretical models and to test the theoretical models empirically using mixtures of inbred lines derived from Yellow Double Dwarf 38 mile (*Sorghum bicolor* (L. Moench)). In this paper we consider the relationship between level of diversity and mean performance. The data relating to stability of performance is reported in a second paper.

Materials and Methods

Experiment 1

The materials used in this study were a population of Double Dwarf milo 38 (hereafter referred to as the base population) derived from a foundation seed lot of this variety provided by the California Crop Improvement Association, and 100 inbred lines (S_7), the progenitors of which were selected at random from the base population. A total of 45 experimental populations, representing 9 distinct levels of genetic diversity, were founded from the above materials as follows:

Group 1 — five randomly chosen inbred lines. These represent the level of within population genetic diversity normal in pure-line varieties.
Group 2 — five unique two-way mixtures.
Group 3 — five unique four-way mixtures.
Groups 4 to 8 — five unique six-, twelve-, twenty-, fifty- and eighty-way mixtures.
Group 9 — five randomly chosen seed samples from the base population of Double Dwarf 38 representing the "diverse" control.

The lines used in each mixture were, so far as possible, chosen at random. However, no line was included more than once in any mixture. Equal proportions of each component were used in all mixtures and each mixture was reconstituted annually. The composition of each of the mixtures will not be presented here because of space requirements; a complete list is given by Marshall (1968).

The 45 experimental populations were grown, using a randomised complete block design with three replications, over a three year period (1965 to 1967 inclusive) at three locations in California: i. University farm, Davis; ii. West Side Field Station; Five Points; and iii. Imperial Valley Field Station, El Centro. These locations vary markedly with respect to climate, soil type and the cultural practices employed. Drilled plantings were made in single row plots, initially 19 feet long and 30 inches apart at Davis and West Side. At Imperial Valley, because of a salinity problem, each plot consisted of two rows 12 inches apart on beds 40 inches apart. After the seedlings emerged the plots were trimmed to 16 feet to ensure that all plots were of equal length. Seeding rates were 8 seeds per foot at Davis and West Side and 6 seeds per foot at Imperial Valley.

A total of 7 characters were recorded for each plot. However, the data for only three of these characters, weight of grain per plot, total number of seeds per plot and seed size, are reported here.

Experiment 2

In this experiment 25 inbred lines, from which the two- to twelve-way mixtures had been constituted, along with an equiproportional mixture of these lines and the base population, were grown at University Farm, Davis, over the same three-year period in a randomised complete block design with three replications. All practical aspects of this study were similar to experiment 1. Each year experiment 2 was sown immediately adjacent to experiment 1 and every effort was made to treat both groups of plots in a like manner to make the results of the two studies as comparable as possible.

Theoretical Results

Relationship between Diversity and Performance in Randomly Constituted Mixtures

Consider a group of l lines or genotypes (l may vary without limit) for which the yield in pure stand of the i^{th} genotype is Y_i and the mean yield of all genotypes is $\overline{Y}\left(=\sum^{l} Y_i/l\right)$ in some specified environment. If a random sample of, say n, genotypes is grown in pure stands in the same environment, the expected mean yield of this sample is also $\overline{Y}$. Further, if the n genotypes are compounded into an equiproportional mixture, the yield of the mixture ($Y_{m,n}$), assuming the environment is completely uniform and genotypes in the mixtures do not interact, is simply the weighted mean yield of the component genotypes $(\overline{Y}_n)$, that is,

$$\overline{Y}_{m,n} = \sum_i p_i Y_i = \overline{Y}_n\,, \tag{1}$$

where p_i is the relative frequency of the i^{th} genotype in the mixture.

Since $p_i = 1/n$ for all i, the expected yield of the mixture is also $\overline{Y}$ and we have,

$$E[Y_{m,n}] = E\Big[\sum_i Y_i\Big]\Big/n = \overline{Y}\,. \tag{2}$$

Thus, under the above assumptions, the expected yield of a mixture is independent of the number of lines it contains.

The assumptions of uniformity of the environment and the absence of competitive interactions among genotypes are, of course, highly unrealistic. Consequently, these restrictions will now be relaxed and we will examine the effects of environmental heterogeneity and certain types of competitive interactions on our previous results. As a first step toward this end we consider the same model as before, except we now specify that: i. the environment contains N different facies or niches, ii. the k^{th} niche occurs with frequency q_k $(k = 1, \ldots, N)$ and iii. the yield of the i^{th} genotype in the k^{th} niche is Y_{ik}. We also specify that all genotypes are initially distributed at random among the N niches. It may be felt that by limiting the latter assumption to the initial distribution of the genotypes among the niches we are ignoring the very real possibility that the distribution of genotypes may be altered during the establishment and development of the plants. However, this is not the case. Changes in relative niche distribution are often, but by no means invariably, due to competitive interactions among genotypes in the population. Yet, in the analysis of competition experiments the results of all such changes, regardless of the underlying cause, are attributed to "interaction effects". This is a matter of necessity rather than choice. Few natural habitats are made up of distinct, recognizable niches. Rather, there is a continuum of subtly different niches. The work of Harper, Williams and Sagar (1965) on the range of microclimates encountered by seeds in the soil, illustrates this point well. As a consequence, it is usually not possible to follow changes in the distribution of genotypes among the niches of an environment, or to determine to what degree such changes are dependent upon competitive interactions. Since the results of changes in relative niche distribution are normally regarded as interaction effects, by making the assumption of absence of competitive interactions among genotypes we imply that such changes do not occur. Thus, taken together, the assumptions of initial random distribution of genotypes and the absence of interactions imply that all individuals, regardless of genotype, are distributed at random among the N niches at all stages at plant development. Under this model the yield of the i^{th} genotype in pure stand is given by

$$Y_i = \Sigma_k\, q_k\, Y_{ik}\,, \tag{3}$$

and the expression for the yield of an n component mixture becomes

$$Y_{m,n} = \sum_{ik}\sum p_i\, q_k\, Y_{ik} = \overline{Y}_n\,. \tag{4}$$

If $p_i = 1/n$ for all i, as before, the expected yield of an n component mixture is $\overline{Y}$. Thus in the absence of interactions among genotypes, genetic diversity imposes no burden on the population, regardless of the degree of heterogeneity of the environment, provided all individuals are distributed at random among the niches of the environment.

If we now relax the assumption that competitive interactions among genotypes are absent, the expression for the yield of a mixture of n lines becomes

$$Y_{m,n} = \sum_i p_i \,(Y_i + I_{i,\cdot}),\ \mathrm{I}_{i,\cdot} \gtrless 0\,, \tag{5}$$

where Y_i is given by (3) above and $\mathrm{I}_{i,\cdot} = \sum_k q_k \,\mathrm{I}_{ik}$, the weighted mean interaction effect of the i^{th} genotype with the $(n-1)$ other genotypes in the mixture over the N niches. In order to determine the relationships between the number of lines in a mixture and its expected yield, it is necessary to specify how the I_{ik} vary with the number or frequency of the components in the mixture. In the absence of a general quantitative description of interaction effects in genetically heterogeneous populations we assume, following Shutz, Brim and Usanis (1968), that they are additive, i.e.,

$$\mathrm{I}_i = \sum_{k,\, i \neq j}\sum q_k \,p_j \,\mathrm{I}_{(i/j,k)} = \sum_{i \neq j} p_j \,\mathrm{I}_{(i/j,\cdot)}\,, \tag{6}$$

where $\mathrm{I}_{(i/j,k)}$ is the interaction response of the i^{th} genotype to the presence of the j^{th} genotype in the k^{th} niche and $\mathrm{I}_{(i/j,\cdot)}$ is the weighted mean interaction response over the N niches.

Substituting (5) and (6) yields:

$$Y_{m,n} = \sum_i p_i \,Y_i + \sum_{i \neq j}\sum p_i \,p_j \,\mathrm{I}_{(i/j,\cdot)}\,. \tag{7}$$

Thus, under this model, the expected yield of a randomly constituted equiproportional mixture of n lines is given by

$$E[Y_{m,n}] = E[Y_i] + (n-1)\,(E[\mathrm{I}_{i/j,\cdot}])/n\,,$$

and therefore

$$E[Y_{m,n}] = \bar{Y} + (n-1)\,\bar{I}/n\,. \tag{8}$$

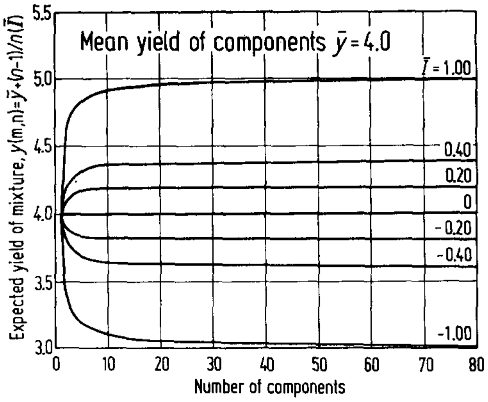

Fig. 1. Relationship between level of diversity and expected mean yield of randomly constituted mixtures assuming interaction effects are additive. In this example the mean pure stand yield of the component lines ($\bar{Y}$) is 4.0 and the average interaction effect between lines ($\bar{\mathrm{I}}$) varies between -1.0 and $+1.0$

The relationship between level of diversity and mean performance is illustrated in Fig. 1 for $\bar{Y} = 4.00$ and $\bar{\mathrm{I}} = 0, \pm 0.20, \pm 0.40$ and ± 1.00 (respectively 0, 5, 10 and 25 per cent of $\bar{Y}$ respectively). For $\bar{\mathrm{I}} \neq 0$, the mean yields of the mixtures rapidly increase or decrease with increasing n and asymptotically approach $(\bar{Y} + \bar{\mathrm{I}})$ as n approaches infinity.

While the above discussion was couched in terms of the relationship between genetic diversity and yield in a single environment, the same conclusions hold for any quantitative measure regardless of its relation to yield, and for any number of environments. In the next section we compare the observed and expected relationships between level of diversity and mean yield for the sorghum mixtures to establish whether the above model is valid for this material.

Experimental Results

Observed Relationship between Level of Diversity and Yield

The means for each character and population over the nine environments in Experiment 1 are summarised in Table 1. There were significant differences among both populations and levels of diversity for all three characters. The weight of grain per plot is greater for level of diversity 9, the base population, than the first eight levels of diversity. On the average, Double Dwarf 38 produced more and heavier seeds than the artificially compounded mixtures. However, even though the base population was more productive than the average inbred line or mixture, it was not as productive as the best line or mixture. Both populations 1 and 11 significantly outperformed Double Dwarf 38. Population 1, an inbred line, was the highest yielding entry in this experiment.

To determine whether the experimental results conform to the theoretical relationship derived above, the regression equation

$$X_1 = \beta_1 + \beta_2 X_2 \qquad \text{where} \qquad X_2 = (n-1)/n$$

was fitted to the data for the first eight levels of diversity. In this equation β_1 estimates the mean yield (or seed size, or seed number) of the inbred lines grown in pure stand and β_2 estimates the mean interaction effect among the 100 inbred lines $(\bar{I})$. The data for Double Dwarf 38 (level of diversity 9) were not included in these calculations. Recent experimental studies (Ainsworth, 1968) have established that the base population contains a substantial amount of heterozygosity for quantitative traits. Consequently, it is impossible to estimate accurately the level of genetic diversity in the base population relative to that in the mixtures of inbred lines. The

Table 1. *Mean yield, seed number and seed size of the 45 populations in experiment 1 averaged over all observations*

Level of diversity	Population	Yield (kgm/plot)	Number of seeds/plot ($\times 10^5$)	Seed size (gm/100 seeds)
1 (inbred lines)	1	3.32	1.21	2.74
	2	3.11	1.18	2.62
	3	2.82	1.07	2.65
	4	2.97	1.14	2.58
	5	2.78	1.05	2.63
	Mean	3.00	1.13	2.64
2 (two-way mixtures)	6	3.09	1.18	2.62
	7	2.93	1.13	2.59
	8	2.98	1.12	2.68
	9	3.04	1.16	2.61
	10	2.92	1.10	2.65
	Mean	2.99	1.14	2.63
3 (four-way mixtures)	11	3.24	1.21	2.66
	12	3.16	1.18	2.67
	13	3.06	1.13	2.70
	14	2.98	1.11	2.66
	15	2.76	1.05	2.63
	Mean	3.04	1.14	2.66
4 (six-way mixtures)	16	2.93	1.12	2.61
	17	3.09	1.12	2.75
	18	3.08	1.16	2.66
	19	2.89	1.07	2.70
	20	2.87	1.05	2.73
	Mean	2.97	1.10	2.69
5 (12-way mixtures)	21	2.93	1.10	2.67
	22	2.99	1.11	2.69
	23	3.01	1.11	2.71
	24	2.92	1.09	2.67
	25	2.89	1.12	2.66
	Mean	2.97	1.11	2.68
6 (20-way mixtures)	26	2.82	1.03	2.75
	27	3.07	1.15	2.65
	28	2.98	1.11	2.67
	29	2.97	1.09	2.71
	30	3.00	1.13	2.65
	Mean	2.97	1.10	2.69
7 50-way mixtures)	31	2.93	1.08	2.71
	32	2.94	1.09	2.70
	33	3.03	1.12	2.70
	34	2.91	1.08	2.69
	35	3.06	1.12	2.72
	Mean	2.97	1.10	2.70
8 (80-way mixtures)	36	3.02	1.12	2.69
	37	2.97	1.12	2.65
	38	2.88	1.07	2.67
	39	3.07	1.17	2.64
	40	3.00	1.13	2.64
	Mean	2.99	1.12	2.66
9 (BP)	41*	3.07	1.14	2.69
LSD (5%) between populations		0.16	0.07	0.05
LSD (5%) between levels of diversity		0.07	0.03	0.02

* The 5 populations of Double Dwarf 38 base population were treated as a single entry with 15 replications.

relationships between level of diversity and the means for each character are shown in Fig. 2.

The estimates of β_2 (or $\bar{I}$) were negative for both yield and the number of seeds per plot but positive for seed size. Thus, it appears that the effects of positive interactions for seed size on yield were more than offset by the negative interactions for seed number. In all cases the estimates of $\bar{I}$ were small and represented only 1.0, 2.3 and 2.6 per cent of the estimates of β_1 or $\bar{Y}$ for yield, seed size and seed number respectively.

The analyses of variance for goodness of fit of the above regression function are given in Table 2. In these analyses, comparison of the mean square for deviations from the specified regression with the within levels of diversity mean square provides a test of the null hypothesis that X_1 and X_2 are linearly related. In addition, comparison of the regression mean square with the residual mean square provides a test of the null hypothesis that $\beta_2 = 0$, assuming the specified linear regression model is correct (Draper and Smith, 1966). If the mean square for deviations from the specified regression is significantly greater than the within levels mean square, then the hypothesis that the yield of a mixture (X_1) is linearly related to $(n - 1)/n$ or X_2 must be rejected. It is then immaterial whether or not the regression is significant because the specified function does not adequately represent the data indicating that one or more of the assumptions underlying the proposed model is invalid.

Table 2 shows that the ratio of the deviations mean square and the within-levels mean square is non significant for all three characters. Thus the specified regression function adequately represents these data. The fact that deviations from the specified regression were not significant does not necessarily mean that the model tested is the correct one. It merely indicates that it is a plausible model which has not been found wanting by these data. Note that the regression is significant for seed size and thus that the null hypothesis, $\beta_2 = 0$, can be rejected in this instance. However, the estimates of β_2 (or $\bar{I}$) were not significantly different from zero for yield and seed number, indicating that values for

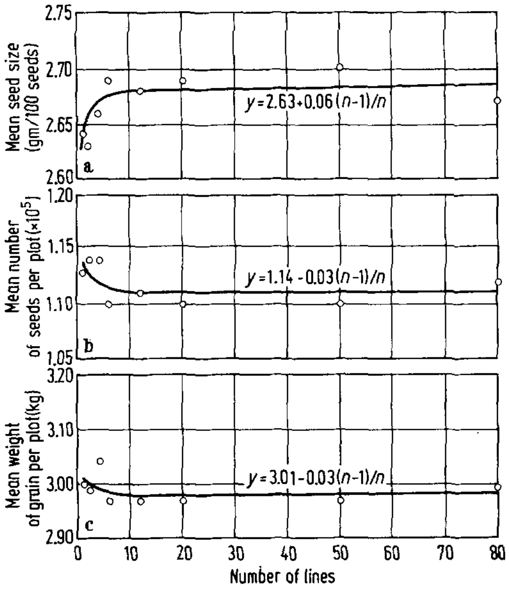

Fig. 2. Observed relationship between level of diversity and: A mean yield; B seed number and; C seed size for the sorghum mixtures

Table 2. *Analyses of variance for goodness of fit of the regression equation $X_1 = B_1 + B_2 X2$, where $X_2 = (n-1)/n$ to the experiment 1 data*

Source variation	d.f.	Mean squares		
		Yield	Seed number	Seed size
Total	39			
Regression	1	0.0038	0.0039	0.0122**
Residual	38	0.0130	0.0018	0.0014
Deviations from specified regression	6	0.0029	0.0012	0.0017
Within levels of diversity	32	0.0149	0.0019	0.0014

* Significant at the 5% probability level.
** Significant at the 1% probability level.

these two characters were independent of the number of lines in the mixture.

Analysis of Interaction Effects

The above results show that the mean interaction effects among lines for grain yield and its components are relatively small. Unfortunately, it is not possible to obtain estimates of the interaction effects in individual populations from these data. Yet, from a practical standpoint, a knowledge of the variation in interaction effects among populations and, in particular, the proportion of mixtures which show high positive interaction effects sufficient to offset the yield disadvantage of the lower yielding components, is far more informative than the mean interaction effect averaged over all populations. We can, however, obtain a limited number of estimates of the interaction effects in individual populations by comparing the observed means for the 20 mixtures in levels of diversity 2 to 5 with their expected values, calculated from the data on the 25 inbred lines in experiment 2, assuming no interactions between lines. The differences between the observed and expected values for each character and population are summarized in Table 3, from which it can be seen that the great majority (15/20) of the mixtures yielded more than the mean of their components. Nevertheless, only one mixture, (population 8 with a 9.3 per cent advantage over its mid-component) yielded significantly more than expected and none of the mixtures yielded significantly more than their better or best component. However, the yield of five of the mixtures (populations 8, 9, 10, 11 and 22) did not differ significantly from their most productive component. The mean difference over all mixtures between the observed and expected yields, although small (1.71 per cent of the mean yield of the component lines), was significant. Table 3 also shows that the superior yields of the artificial mixtures came from positive interactions among lines for seed size rather than for seed number.

Table 3. *Difference between observed yield, seed number and seed size of mixtures in levels of diversity 2 to 5 and their expected values*

Level of diversity	Population	Yield	Seed number ($\times 10^5$)	Seed size
2 (two-way mixtures)	6	−0.03	−0.04	+0.05
	7	+0.04	+0.03	−0.03
	8	+0.27*	+0.08	+0.05
	9	+0.16	+0.03	+0.09
	10	+0.15	+0.04	+0.02
	Mean	+0.12*	+0.03	+0.04
3 (four-way mixtures)	11	+0.14	+0.02	+0.07
	12	+0.06	−0.03	+0.10
	13	+0.11	+0.01	+0.09
	14	+0.13	0.00	+0.10
	15	0.00	+0.03	−0.09
	Mean	+0.09	+0.01	+0.07*
4 six-way mixtures)	16	+0.09	+0.03	+0.03
	17	+0.07	+0.04	+0.10
	18	−0.09	−0.07	+0.06
	19	+0.03	−0.04	+0.21**
	20	−0.01	−0.05	+0.13*
	Mean	+0.02	−0.02	+0.11**
5 (12-way mixtures)	21	−0.16	−0.08	+0.02
	22	+0.14	+0.06	+0.01
	23	+0.01	−0.04	+0.08
	24	+0.03	0.00	0.00
	25	+0.04	+0.01	+0.01
	Mean	+0.01	−0.01	+0.02
	Grand Mean	+0.05*	0.00	+0.06**

* Significant at 5% probability level.
** Significant at 1% probability level.

The data in Table 3 can also be used to estimate the second and higher order interaction effects in the 4-, 6- and 12-way mixtures and, hence, to test the validity of the assumption that such interaction

Table 4. *Estimates of first and higher order components of mean interaction effect for levels of diversity 2 to 5 and their standard errors (s.e.)*

Level of diversity	Yield				Seed number ($\times 10^5$)				Seed size			
	First order*	S.E.	Higher orders†	S.E.	First order*	S.E.	Higher orders	S.E.	First order*	S.E.	Higher orders	S.E.
2	0.12	0.053	—	—	0.03	0.024	—	—	0.04	0.025	—	—
3	0.18	0.079	−0.09	0.130	0.05	0.036	−0.04	0.044	0.06	0.037	0.01	0.032
4	0.20	0.088	−0.18	0.138	0.05	0.040	−0.07	0.063	0.07	0.041	0.04	0.045
5	0.22	0.097	−0.21	0.144	0.06	0.044	−0.07	0.063	0.07	0.066	−0.01	0.063

* Estimated as $(n-1)\,\overline{I}_{(i/j)}/n$ where n is the number of lines in the mixture; $\overline{I}_{(i/j)}$ was estimated as twice the average difference between observed and expected yields of two-way mixtures.

† $\overline{\Delta}_n - \overline{D}_n - (n-1)\,\overline{I}_{(i/j)}/n$

effects are unimportant. Under the assumption of additive interaction effects, the expression for the yield of an n-component equiproportional mixture is, from (8) above,

$$Y_{m,n} = \overline{Y}_n + (n-1)\,\overline{I}_{(i/j)}/n\,,$$

where $\overline{Y}_n$ is the mean yield of the n lines in pure stand and $\overline{I}_{(i/j)}$ their average interaction effect. However, if the assumption of additivity is relaxed, we can write

$$Y_{m,n} = \overline{Y}_n + (n-1)\,\overline{I}_{(i/j)}/n + \Delta_n\,, \tag{9}$$

where Δ_n is a measure of the non-additive interaction effects.

In two-component mixtures $\Delta_n = 0$ by definition. Thus, for a two-component mixture

$$D = Y_{m,n} - \overline{Y}_n = \overline{I}_{(i/j)}/2 \tag{10}$$

and

$$\overline{I}_{(i,j)} = 2\,D\,,$$

where D is the difference between the observed yield of a mixture and its expected value.

In higher order mixtures $\Delta_n \gtreqless 0$, hence

$$D = (n-1)\,\overline{I}_{(i/j)}/n + \Delta_n\,, \tag{12}$$

and

$$\Delta_n = D - (n-1)\,\overline{I}_{(i/j)}/n\,.$$

Thus, provided estimates of D and the $\overline{I}_{(i/j)}$ are available, we can determine the magnitude of non-additive interaction effects in higher order mixtures.

As noted by Shutz, Brim and Usanis (1968) invoking additive interaction effects implies: i. that the interaction effect of the i^{th} genotype, G_i, in competition with G_j is a linear function of its frequency; and ii. that second and higher order interactions are absent. In general, the effects of deviations from both these assumptions will be confounded in estimates of Δn. However, in equiproportional mixtures where the frequencies of any pair of genotypes relative to each other are constant (for example, for two genotypes X_i and X_j with frequencies $p_i = p_j = l/n$ and $p_i/(p_i + p_j) = 1/2$ regardless of n), any deviations from additivity in interactions effects can be attributed solely to second and higher order interactions. Consequently, provided we limit our attention to equiproportional mixtures, Δ_n becomes a measure of higher order interaction effects.

The estimates of the average first and higher order components of total interaction effect for levels of diversity 2 to 5, calculated using the above procedure, are given in Table 4. Although many of the estimates are not significantly different from zero, it will be noted that the first order interaction effects are consistently positive for all three characters whereas the higher order interaction effects are consistently negative for yield and seed number and increase markedly with increasing numbers of lines in the mixtures. For seed size two of the estimates are positive while one is negative and there appears to be no relationship between the magnitude of the estimate and level of diversity. The data thus suggest that, for yield and seed number, second and higher order interaction effects are often as large, or larger, than their first order counterparts and further that they are more likely to be negative than positive.

Discussion

Relationship between Level of Diversity and Yield

The theoretical model developed here leads to the conclusion that the level of genetic diversity and yield of randomly constituted equiproportional mixtures are simply related. The observed relationship between number of components and mean yield for the sorghum mixtures supported this conclusion. However, more detailed analyses of intergenotypic interactions in the sorghum mixtures, which indicated that higher order interaction effects were often as great, or greater, than their first order counterparts, suggest that diversity and yield were complexly related and raised severe doubts as to the validity of the proposed model.

Other studies also indicate that genetic diversity and productivity are complexly related (e.g. Allard, 1961; Frey and Maldonado, 1967; Rasmusson, 1968; Clay and Allard, 1969) and suggest that one, or more, of the assumptions underlying the proposed model is unrealistic. These assumptions are:

i. All individuals, regardless of genotype, are initially distributed at random among the niches of the environment,

ii. the interaction effect of the i^{th} genotype, G_i, in combination with genotype G_j is a linear function of the frequency of G_j, and

iii. the net effect of interactions of a given genotype say G_1, with the other genotypes in the mixture is equal to the sum of the interactions of G_1, with G_2, G_1 with $G_3, \ldots,$ G_1 with G_n. This is equivalent to assuming that the effects of higher order interactions among genotypes are zero.

Assumptions ii. and iii. together imply that the interaction effects are additive.

The first assumption will seldom be met in natural populations which often show marked differentiation over relatively small distances (e.g. Bradshaw, 1952, 1954; Allard *et al*, 1972). However, it is met in the great majority of drill-sown annual crop plants such as grain sorghum where the seeds are distributed at random with respect to genotype down the rows.

With respect to the second assumption, data presented by Sakai (1955, 1957) indicated that competitive responses in both rice and barley were linear functions of the frequency of competing genotypes. Similar results were reported by Shutz and Brim (1967) for a range of soybean genotypes and Allard and Adams (1969) for a range of wheat and barley genotypes. These results suggest that the assumption of a linear relationship between competitive response and the frequency of competing genotypes may often be justified in crop plants. Thus it is also unlikely that this assumption will detract greatly from the generality of the proposed model. Further, all investigators who have examined the relationship between numbers of components and mean yield in simple line blends have restricted their attention to equiproportional mixtures in which the frequencies of any pair of genotypes relative to each other remain constant regardless of the numbers of components in the mixtures. Consequently, the failure of published empirical observations to conform to the expectations of an additive interaction effects model cannot be attributed to non-linear competitive responses with changes in genotypic frequencies.

If the above conclusions are valid the discrepancy between our theoretical model and the bulk of the published experimental data can be attributed to substantial effects of second and higher order interactions on the productivity of mixtures containing three or more components. This conclusion has important practical implications. In particular, it means that models based on the assumption of additive interaction effects may be of little value in predicting the performance of line blends in crop species. Unfortunately, the lack of fundamental information on higher-order interaction effects in crop plants makes it difficult to suggest changes which would increase the realism of such models and improve their predictive power. Obviously, this information will only come from studies specifically designed to further our understanding of the magnitude and nature of higher order intergenotypic interactions. The apparent importance of these interactions in heterogeneous populations suggests such studies should receive greater emphasis in the future than they have in the past.

Commercial Potential of Multiline Mixtures

Reconstitutable multiline varieties will gain widespread commercial acceptance only if it can be demonstrated that they are clearly superior to conventional pure-line varieties in terms of yield, stability of yield or disease tolerance. With respect to yield, most published studies agree in indicating that mixtures often, but by no means invariably, outperform their average component. However, they seldom outperform their better or best component (Simmonds, 1962; Marshall, 1968). The present results closely followed this established trend. Consequently, it would appear that while favorable interaction effects are relatively common in crop species they are seldom of sufficient magnitude to offset the burden imposed on heterogeneous populations by the lower yielding genotypes. Nevertheless, a number of investigators remain optimistic about the commercial potential of multiline blends. These investigators acknowledge the fact that, in the majority of studies reported in the literature, the yield advantage of mixtures over the mean of their component lines has been small. However, they argue that this result is not entirely unexpected, since the mixtures studied were usually compounded more or less randomly from good local varieties without regard to their potential for favorable interactions. They suggest, following Simmonds (1962), that a systematic search for combinations of genotypes which show marked favorable interactions should lead to substantially greater gains in productivity than have been reported to date.

However, the practical plant breeder must consider not only whether it is possible to construct mixtures which outyield elite single-line varieties, but whether the yield advantage offered by such mixtures is great enough to offset the cost of their initial development and the increased cost of seedstock preparation. Since only a small proportion of randomly constituted blends significantly outyield elite pure-line varieties, the cost of developing a commercially acceptable multiline mix is likely to be substantial. Moreover, there is little evidence to suggest that the potential yield advantage of mixtures, even those constructed on the basis of an *a priori* knowledge of the pure stand yield and interaction effects of the components (e.g. Jensen, 1965; Brim and Shutz, 1968) are great enough to justify this cost. As a consequence, it seems reasonable to suggest that multiline blends are unlikely to enjoy widespread commercial success, unless they offer substantial additional advantages over single-line varieties in terms of stability of yield and/or disease tolerance. The effects of genetic diversity on stability of yield will be considered in some detail both theoretically and experimentally, in the second paper of this series.

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