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Population Structure and Performance in Wheat

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INTRODUCTION

Considerable attention has been given recently to advantages in yield and stability of performance for genetically diverse populations and the possible use of heterosis from intervarietal hybrids of wheat. Both of these facets of population structure are not conventional in the sense of the usual agricultural variety. The utilization of heterosis in wheat is beset with several difficulties relating to hybrid seed production and it may be necessary to utilize advanced generation hybrids or populations derived from more than two parents, such as three-way or double crosses. Evidence from several crops indicates that individual and population buffering in genetically diverse populations results in a more stabilized production and, in some cases, a higher yield (see ALLARD and BRADSHAW (1964) for review). Genetic diversity can be attained through the mixture of homozygous types as BORLAUG (1959) and JENSEN (1965), among others, have proposed or through greater use of heterozygosity as ALLARD and HANSCHE (1964) have suggested. Yield levels of the F_2 generation in wheat have been higher than the midparent and better parent in some cases (e.g., FONSECA and PATTERSON (1968)). SIMMONDS (1962) reviewed the existing data on the performance of varietal mixtures of cereal crops. He concluded that the performance of mixtures was often equal to the midcomponent, sometimes higher, and occasionally even higher than the best component. The yield advantage over the midcomponent for a large number of experiments was 3 to 5 per cent. Heterogeneous populations also are commonly better buffered against environmental fluctuations as evidenced by smaller genotype-environment interaction variances (see SIMMONDS (1962) and ALLARD (1961)). With barley FINLAY (1964) found that F_2 populations were phenotypically more stable and had higher yield levels than the parents. This paper also presents an analysis of stability and level of performance of F_2 populations as well as simple mixtures.

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EXPERIMENTAL DETAILS

A seven-parent genetic and mechanical diallel was studied in three environments in Tennessee. F_2 populations and 1 : 1 mixtures were derived using the winter wheat varieties listed in TABLE 1. The performance of the F_1 hybrids of this diallel cross had been previously studied (GYAWALI *et al.*, 1968) in which a wide range of heterosis was found. The parental varieties differ widely in time of maturity and plant height (M, K, K62, and T are early and moderately short). T is a hard winter wheat and the remaining varieties have soft kernel texture. K62 is a hessian fly resistant backcross derivative of K and is phenotypically very similar to K.

TABLE 1. Stability parameters for parental varieties and for F_2 or mixture parental arrays. See text for identification of *b*, *W*, and *D*.

Variety	Parental value			Parental array mean					
				b		W		D	
	b	W	D	F_2	Mix	F_2	Mix	F_2	Mix
Seneca (S)	0.91	1032	936	1.09	0.98	3399	2796	1474	635
Monon (M)	1.57	3751	8	1.08	1.13	3115	1210	919	412
Knox 62 (K62)	0.99	233	231	1.03	0.92	2298	2680	1835	391
Knox (K)	0.25	7021	337	0.98	0.82	2076	1213	847	346
Genesee (G)	1.62	4388	2	1.01	1.30	3200	2699	1627	935
Tenn. 9 (T9)	1.82	8463	645	0.97	1.07	3339	1296	2175	248
Triumph (T)	0.32	5437	4	0.72	0.72	1783	3353	486	784

The experiment consisted of four replications of four-row plots 3 m long at Knoxville in 1967 and Springfield in 1966 and 1967. Seeding rates were established by seed number to a rate approximating 85 kg/ha. The average grain yields of all entries (7 parents, 21 F_2's, and 21 mixtures) at the above three locations were 1400, 2300, and 1710 kg/ha, respectively. Thus the yield of these three environments was at a moderately low level. All yield data presented here are given as grams per plot.

LEVEL OF PERFORMANCE

The yields of the individual populations, averaged over the three environments, are given in TABLE 2. It is evident that the yields of the F_2 populations were higher than the mixtures in most cases and the difference between the two groups was 4.4 per cent, a significant difference (TABLE 3 and Figure 1). The F_2 populations were also generally higher than the midparent, but the mixtures were not. However, the F_2 and mixture yields were significantly correlated (.62**) and the three F_2 parental combinations (M-K, K-T9, and T9-T) which were significantly higher than the midparent also were higher than the midparent in the corresponding mixtures (TABLE 2). Two F_2 populations (S-T9 and K-T9) were significantly higher than K62, the best parent of the set. It is worthwhile noting that F_1 hybrids with T9 produced the highest yield

TABLE 2. Yield in grams per plot and as per cent of the midparent (MP) and stability parameters for 21 F_2 and 21 mixture populations.

Variety / Combination	Yield, grams: F_2	Yield, grams: F_2−Mix	Yield, % MP: F_2	Yield, % MP: Mix	Stability parameter b: F_2	Stability parameter b: Mix	Stability parameter W: F_2	Stability parameter W: Mix	Stability parameter D: F_2	Stability parameter D: Mix
S M	296	−21	100	109[a]	1.71	1.06	5870	265	1	228
S K62	334	40	105	92[a]	1.01	1.05	5138	1952	5140	1920
S K	314	−9	106	109[a]	0.64	1.06	1511	221	1	186
S G	346	22	110[a]	103	1.54	1.76	3308	7652	7	886
S T9	382	−3	97	98	0.83	0.55	3509	2868	3166	557
S T	307	5	103	102	0.79	0.43	1059	3810	528	34
M K62	305	18	101	96	0.76	1.10	682	187	39	64
M K	333	22	120*	112*	1.51	0.70	3081	2640	0	1546
M G	297	29	100	90[a]	1.24	1.42	1676	2184	983	95
M T9	277	6	102	100	0.64	1.30	5885	1610	4402	536
M T	285	4	102	101	0.65	1.18	1493	371	91	4
K62 K	297	2	99	98	0.84	0.61	2382	2039	2068	237
K62 G	332	10	104	101	1.26	1.25	2283	752	1502	0
K62 T9	321	23	110[a]	102	1.30	1.40	1710	1971	674	101
K62 T	296	8	98	96	0.99	0.11	1594	9180	1588	25
K G	308	31	104	93	0.67	1.07	2772	58	2477	0
K T9	345	45	126**	110[a]	1.40	0.90	2095	196	309	78
K T	277	−6	101	102	0.82	0.58	616	2121	229	30
G T9	310	16	102	101	0.94	1.28	4465	1019	4407	119
G T	309	−9	104	107	0.39	1.03	4698	4529	385	4512
T9 T	323	37	120*	105	0.69	0.97	1238	109	94	97
Mean	309	13	105	101						

* .01 < P <.05, ** P < .01, [a] greater than SE = 22 grams.

(GYAWALI *et al.*, 1968). T9 is not a particularly high yielding variety but its good combining ability carried through to the F_2 generation.

The F_2 and mixture populations were analysed separately and combined for general and specific combining ability according to COCKERHAM's (1963) method (TABLE 3). Only the specific combining ability effect was significant for F_2's when the two groups were analysed separately. In the combined analysis the maternal and reciprocal effects are of greatest interest. The maternal effect, representing differences between mixtures and F_2's (in this case the mixtures were used as reciprocal crosses in the analysis), was significant, but the reciprocal effect was not. In the yield of the parental arrays (Figure 2) the superiority of F_2's over mixtures is clearly seen and also that for five of seven varieties the mean F_2 performance was better than the common parent. Also note that none of the F_2 arrays were better than K62 and that the mixture arrays were about equally better and poorer than the parents.

STABILITY OF PERFORMANCE

Stability of performance is difficult to assess because genotype or population responses in a large number of environments are required. However, it can be argued that useful comparisons can be made if stability of one genotype or population is measured relative to another. Three measures of stability were used in this study. The regression of variety performance on site mean yield (b), used by FINLAY and WILKINSON (1963) and FINLAY (1964), and the

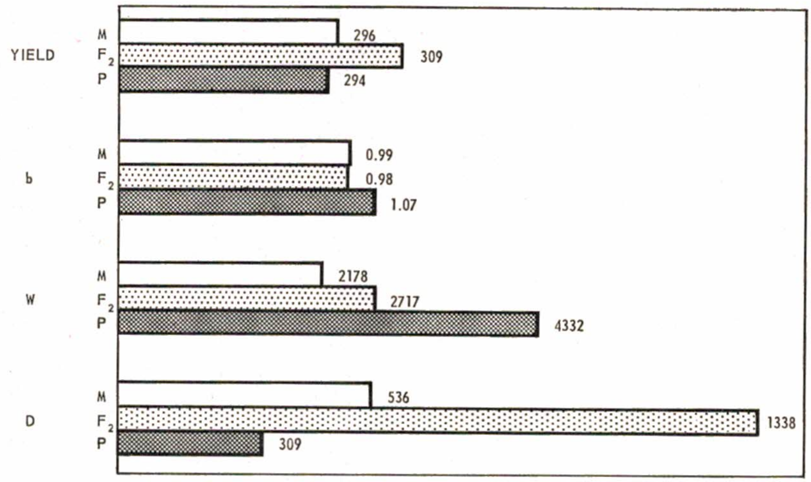

FIG. 1. Mean yield and stability parameters for mixtures (M), F_2 populations, and parents (P). *b, W,* and *D* are defined in the text.

deviation of the observed from predicted yields $D = S\hat{\delta}^2_{ij}$, used by EBERHART and RUSSELL (1966) provide useful measures of stability. This same regression technique was used by MOOERS (1921, 1933) in Tennessee for open-pollinated corn varieties, although he did not quantify the method as it is now known. A third parameter *W*, developed by WRICKE (1962, 1966) and called ecovalence, was used in this study. *W* is the contribution of each genotype to the genotype-environment interaction sum of squares.

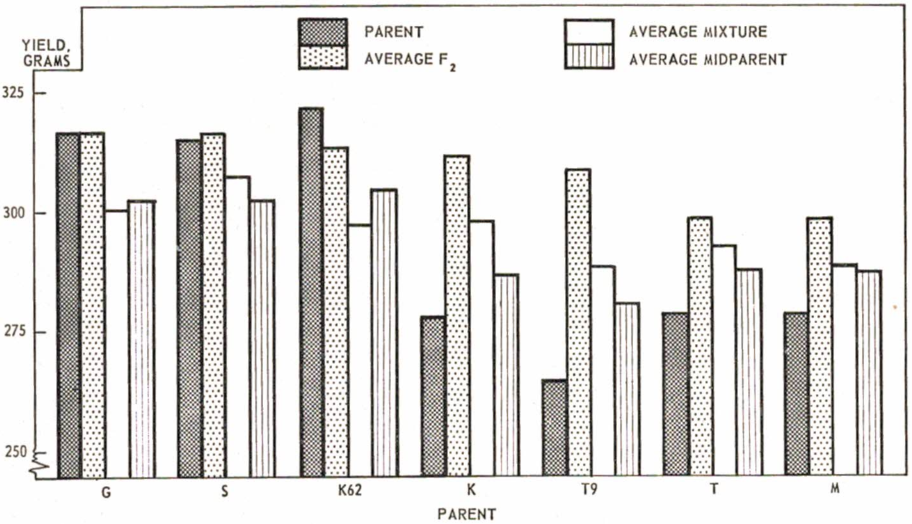

FIG. 2. Parental mean and array mean yield for mixtures, F_2's, and midparents. Parent variety abbreviations are given in TABLE 1.

The assessment of stability in the present study must be considered tentative because only a few environments were studied. The main comparisons among F_2's, mixtures, and parents may have some utility since they are based on all entries of the diallel. Each of the three groups showed significant interaction with the environments (TABLE 3). W values for each parent, F_2, and mixture (TABLES 1 and 2) reveal wide variation as would be expected for a limited number of environments; however, the mean values for all members of each group (Figure 1) show that the order of stability is $M > F_2 > P$. W for mixtures was considerably smaller than F_2's even though one combination (K62-T) had a very large value.

TABLE 3. Mean squares for grain yield from the analyses of variance of parents, of F_2's, and mixtures from a seven-parent genetic and mechanical diallel cross studied in three environments.

Source of variation	All genotypes	F_2's only	Mixtures only	Parents only
Genotypes	5048**	5130*	3781	6553*
Genotype × environ	5496**	5549**	4555*	9661**
Error	2842	2631	2879	2677
Combining ability[a]				
Maternal[b]	9097**			
General	6943*	4466	3843	
Specific	6900**	5565*	3463	
Reciprocal	273			

[a]parents not include, [b]F_2's vs. mixtures, *.01 $<P<$ .05, **$P<$ .01.

Regression coefficients, also highly variable, showed that both F_2's, mixtures, and parents had b-values approximating 1.0 (Figure 1), indicating average stability (FINLAY and WILKINSON, 1963). The deviations from regression D indicated that the predicted yields of the parents agreed quite well with observed, but that the D-values for F_2's were about four times larger than the parents and about two times larger than the mixtures. For two of the three stability parameters the mixtures were apparently more stable, on the average, than F_2's.

DISCUSSION

Generalization from the results of this small study is hazardous and at best should be considered relevant only to low yield conditions. The relationship for yield was $F_2 > M = P$, whereas, especially for the parents, the results for stability were somewhat indeterminant: $M > F_2 > P$ or $P > M > F_2$. The increased stability of mixtures over F_2's was quite obvious and the reason for this is obscure. Wheat has evolved primarily as mixtures of homozygotes rather than through heterogeneity obtained by high levels of heterozygosity, which might suggest that the heterozygosity of an F_2 population is not optimum for high stability. Regarding the difference of level of performance of F_2's compared with mixtures it is not possible to determine the basic causes. If heterogeneity in some varietal combinations results in mutual facilitation, such as with the M-K or K-T9 mixtures (12 and 10 per cent, TABLE 2), this effect might also be expected in segregating populations. The gene frequency in F_2's and mixtures is the same so the difference in performance of F_2 vs. mixture would then represent genetic effects due to dominance, epistasis, or linkage. This difference for M-K and K-T9 was 8 and 16 per cent, respectively, and 4 per cent for all populations. This amount would be expected to approach zero with selfing and therefore may be examined experimentally.

The agricultural use of mixtures, even though a small yield advantage over the midcomponent can be realized and some increased stability is likely to be attained, is not attractive at present because these benefits are small and probably would not outweigh the cost of seedstock preparation. More promising, however, is the use of advanced generations of intervarietal crosses (two or more parents) because of the possibility of higher yields and selection of populations for greater stability. As an example from this study, the F_2 population T9-T produced high yield and had above average stability for all three measures of stability.

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