

SELECTION FOR WIDE AND SPECIFIC ADAPTATION
IN THREE POPULATIONS OF CORN (ZEA MAYS L.)

by

MOHAMMAD SALIM KHAN

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Approved by:

Clyde E. Wasson
Major Professor

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INTRODUCTION

Corn is one of the most important food crops, but its yield per acre is still low in many countries. In some of the developing countries where hybrid corn seed is not produced or available, corn synthetics or composites of wide adaptability can be successfully used. Widely adapted synthetics with high yield capability can easily replace the low yielding local corn varieties in those areas. In addition, synthetics adapted to specific sites may give higher yields in some areas.

However, cultivars, hybrids or other forms of improved corn may not perform uniformly at different locations or in different years. Variations in phenotypic response may be expressed in genotype x environment interactions. Extensive testing of genotypes at more than one location and in more than one year is required for evaluations whenever large genotype x environment interactions exist. The improvement of material specifically adapted for each of many different environments may not be feasible because of the large number of possible genotypes required for each corresponding genotype x environment interaction. However, the solution to the problem may be simplified because there is strong evidence which suggests that genotypes exist which are adapted to a

wide range of environments.

Several methods have been developed to characterize such interactions in the past. Conventional analysis of variance may not provide the breeder an adequate means of recognizing or evaluating the characteristics of interest. In general, the aim of the plant breeder is to obtain high mean yield over different environments and select those genotypes which show less interaction or response to the environments. Stability parameters suggested by Eberhart and Russell (1966) have been widely used to identify and classify adaptability of varieties.

Scott (1967) defined a stable genotype in two different ways: (1) a genotype which shows least yield variation over all environments tested; such a genotype may have less yield reduction in unfavorable environments, and (2) a genotype which does not change its relative ranking with other genotypes tested across many environments; such a genotype may be high yielding in favorable growing conditions.

The objectives of this study were (1) to raise yield levels for a wide range of environments in three populations of corn by developing and applying improved selection criteria; (2) to compare performance of synthetics developed for both specific and wide adaptation within and across locations.

LITERATURE REVIEW

Several intrapopulation improvement procedures have been used in the past. Mass selection is the easiest and the least expensive procedure for improving crop plants. The relative ineffectiveness of mass selection in increasing crop yields is caused by inability to identify superior genotypes from their phenotypic appearance because of large genotype-environment interactions. Gardner (1961) introduced a refined mass selection scheme to reduce environmental variation by selection among plants within small subdivision of the field. These refinements improved the yield of 'Hays Golden' variety of corn (Zea mays L.) at the rate of about three percent per generation for seventeen cycles (Gardner, 1973).

Full-sib family, half-sib progeny test, and S_1 progeny test in which evaluation is based on progeny performance are other intrapopulation selection procedures. Moll and Stuber (1971) reported progress from full-sib family selection in four corn populations during seven cycles of selection. da Silva and Lonnquist (1968) obtained good agreement between expected and realized gains in yield of corn in a comparison between full-sib selection and half-sib progeny tests. The higher selection intensity among full-sib families than half-sib families was responsible for greater response in full-sib

selection.

Empig et al. (1972) reported that the choice of tester used for half-sib family production affected the kind of selection response expected. Allison and Curnow (1966) concluded that population improvement would be best accomplished when the parental population was the tester. Their conclusion was based on theoretical considerations.

The importance of additive genetic variance for progress from intrapopulation selection has been emphasized by numerous workers. Moll and Robinson (1967) indicated that additive genetic variance was predominant for most agronomic characters in corn. Shauman (1970) reported yield gains from an intrapopulation improvement scheme and emphasized the presence of considerable amount of additive genetic variance. Lonquist (1964) indicated the presence of additive genetic variance in open pollinated varieties of corn. Differences in general combining ability of the inbred lines using broad genetic testers were attributed mainly to this genetic variance component.

Epistatic genetic effects appeared not to be an important portion of genetic variance in corn populations (Chi et al., 1969; Stuber et al., 1966). However, Wright et al. (1971), Russell and Eberhart (1970), and Stuber and Moll

(1971) reported significant epistasis in various corn hybrids. Epistasis generally formed a small portion of total genetic variability in most other studies with corn populations. Sprague (1964) obtained greater estimates of dominance genetic variance than of additive components in two corn varieties. However, he thought that intrapopulation improvement was possible in these populations.

Eberhart et al. (1966) reported additive genetic variance was the largest portion of the total variance for seven characters studied in two corn populations. Similarly, Hallauer and Wright (1967) reported estimated genetic variability for nine traits, including yield in an open pollinated corn variety. Estimates for additive genetic variance were greatest for all traits in their study. Compton et al. (1965) obtained higher genetic variance estimates in two open pollinated varieties of corn from inter-variety families than in varieties from intra-variety families.

Valid performance predictions of a genotype depend on accurate evaluation of genotypic values. Evaluations must be made on phenotypes that are the product of genetic and non-genetic effects. Interactions between genetic and non-genetic effects are called genotype-environment interactions. They reduce the correlation between genotype and phenotype with the result that valid inferences become complicated. Comstock

and Moll (1963) reported statistically significant genotype-environment interactions that reduced progress from selection. Allard and Bradshaw (1964) classified environmental variation into two types, predictable such as climate, soil type and day length, and unpredictable such as distribution and amount of precipitation, temperature changes, and insect or disease infestation. They emphasized that unpredictable variation is more important than predictable variation. Similarly, Finlay and Wilkinson (1963) found seasonal variations were more important than edaphic factors in their adaptation study with barley. Jensen (1952), in a study with oats, suggested multi-line oats varieties were more stable in adaptation, yielding ability and disease resistance than pure line varieties. Allard and Bradshaw (1964) suggested heterozygous and heterogeneous populations were best means of producing varieties that interact less with the environment.

However, Rowe and Andrew (1964) found higher variety-environment variance for yield, plant height and ear height of five inbred lines of corn and their ten possible F_1 combinations than for the segregating generations derived from them. No relation between the variance component and the heterozygosity level of the entries was found.

Sprague and Federer (1951) indicated double crosses were superior to single crosses in wide adaptation. Similarly,

Eberhart, Russell and Penny (1964) obtained significantly higher genotype-year interactions for single crosses than for three-way crosses of corn. However, they thought that some single crosses may have as much or more phenotypic stability than the most stable three-way or double cross.

Scott (1967) showed progress in selecting for yield stability in corn hybrids grown in a number of environments, indicating that genotypic differences exist for yield stability in corn.

Although genetic effects are modified by environmental effects, several workers observed a linear relation between the performance of genotypes in different environments (Finlay and Wilkinson, 1963; Rowe and Andrew, 1964; Eberhart and Russell, 1966). Regression techniques have been suggested and used by research workers to measure phenotypic stability (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Freeman and Perkins, 1971; Perkins and Jinks, 1973). Eberhart and Russell (1966) suggested regression technique for evaluating stability by using two parameters, regression coefficient (b) and the deviation from regression line (S^2_d). Breese (1969), from a study of five populations of Dactylis glomerata, concluded that deviation from regression of Eberhart and Russell (1966) was an important consideration for stability. Jowell (1972), in a study with sorghum, compared the stability evaluation method of Eberhart and Russell (1966) with other methods

and found the Eberhart and Russell method was more informative.

Stuber et al. (1973) obtained correlation of performance of a number of entries in one environment with their performances in other environments to select more stable genotypes. Large positive values of correlations indicated small genotype-environmental interactions, whereas the converse occurred when the magnitude of variance components attributed to such interactions was evaluated.

Many experiments with corn provide significant estimates of genotype-environment interaction variance components for most of the traits studied. Estimates of genotype-environment variance components are larger than estimates of genetic variances (Moll and Robinson, 1967; Stuber and Moll, 1971). Both additive and non-additive effects had significant interactions with environment. Second-order interactions appeared to be greater than genotype-location or genotype-year effects. Otsuka et al. (1972) and Stuber et al. (1973) reported greater biases from genotype-environment interaction effects than from epistatic effects in a single environment. Biases in two or more environments were equal. Lonquist (1967) pointed out that variance estimates from tests with corn in a single environment were biased and estimates of variances based on tests in more than one environment were also biased, depending on the distribution of experiments in time and space. However,

he thought that unbiased estimates from experiments in more than one year or more than one location are extremely limited.

Improvement in performance of a population with selection may be associated with changes in the magnitude of genetic variance. Several studies with corn indicated little change in genetic variance with selection for characters such as yield, which is controlled by many loci, each with small effects (Horner et al., 1973; Lonnquist et al., 1966; Matzinger et al., 1972; Moll and Robinson, 1966). Moll and Stuber (1971), in a selection study with corn, and Matzinger and Wersman (1968), in tobacco, found linear response from selection. Good agreement of realized response with expected response indicated virtually no change in genetic variances.

However, da Silva and Lonnquist (1968) reported decreased genetic variance with selection. Lonnquist et al. (1966) obtained no change in genetic variance after six cycles of mass selection in corn, but Harris et al. (1972) reported decreased genetic variability after nine generations of selection. Dudley and Lambert (1969) observed significant genetic variability still remained in four strains of corn after sixty-five generations of selection for oil and protein percent.

When expected and observed correlated responses and direct responses are compared, the former responses have been

less consistent than the latter responses. Matzinger and Wersman (1968) reported agreement of realized and expected correlated responses for leaf weight in tobacco after four cycles of selection, but correlated responses were not linear over selection cycles. In another experiment with tobacco, realized and expected responses agreed poorly (Matzinger, et al. 1972).

Moll and Robinson (1966), in a yield test of corn, observed good agreement between observed and expected response for number of ears per plant but poor agreement for plant height and days to tasseling. Horner et al. (1973) and Russell et al. (1973), in experiments with corn, showed good agreement between realized and expected correlated responses for yield and number of ears per plant, but variable and poor responses for ear height and grain yield. Searle (1965) reported tables of minimum heritabilities and correlations for facilitating indirect selection. High positive correlation of a trait having high heritability with a trait having low heritability may result in indirect improvement of the second trait. However, discrepancies between expected and correlated observed responses reduce confidence in indirect selection.

Several workers used selection indices instead of indirect selection to apply correlation of traits more

efficiently. Brim et al. (1959) reported a number of indices to improve soybean yields. However, they discussed several errors that might occur during estimation of statistics for indices. Elston (1963) suggested a multiplicative index that is independent of weights. Subandi et al. (1973) demonstrated that a multiplicative index was as efficient as a weighted index and was much simpler.

MATERIALS AND METHODS

Three corn populations were used: Kansas Drought Synthetic (KDS), Mex-Mix (MM), and Amarillo Bajio (AB). KDS, derived from temperate germ plasm, is a composite of Kansas inbred lines which showed best drought resistance from among a number of lines in previous tests under moderate to severe drought conditions in Kansas. Over 400 ears were selected from an isolated planting of KDS at Manhattan, Kansas, to produce half-sib families at Tlaltizapan, Mexico.

Mex-Mix was derived from a mixture of temperate, sub-tropical and mostly tropical germ plasm. Slight selection pressure for plant height was exercised and some selection for yield efficiency (YE) was made with the realization that selection was based on one location. Six hundred plants were selfed and 400 S_1 ears from plants which showed a favorable grain weight per unit of leaf area (YE) were harvested.

Amarillo Bajio contains a mixture of temperate and tropical (Carribean) germ plasm. Amarillo Bajio and Mex-Mix were supplied by CIMMYT (International Maize and Wheat Improvement Center), Mexico.

Approximately 400 ears of the KDS and MM populations were planted at Tlaltizapan, Mexico, during winter, 1973,

to develop families for yield trials at several locations in 1974. Each population was isolated and each ear was planted as a female row. A balanced composite for male rows was made by mixing equal number of seeds from each family for a given population. This produced half-sib seed on the female rows for progeny testing.

One-hundred families in each population were planted at Manhattan and St. John, Kansas, and El Batan, Tlaltizapan and Poza Rica, Mexico in 1974. Two replications in two-row plots five m long with 75 cm (30 in) between rows and 24 cm (9.5 in) between plants were used at each location. A randomized complete block design was used at all locations. Two-hundred kg per ha of N fertilizer was used at all locations. In addition, 16 kg/ha of P and 13 kg/ha of K were used at St. John in both years.

The soil at Manhattan is silt loam with slightly alkaline reaction. The soil at St. John is fine sand.

Tlaltizapan, Mexico, is situated approximately 19° N latitude at 940 m elevation. The soil is alkaline and deficiency symptoms resembling Mg were observed on some families in each population. One hundred kg/ha each of N and P_2O_5 were applied before planting and 150 kg/ha N was applied in two applications 6 weeks after planting and before

tasseling. All tests were grown under irrigation at all locations in both years.

Leaf area of four random competitive plants in each family was measured after pollen shed at Manhattan and Tlatizapan in 1974. Area (A) of each leaf was estimated by the formula $A = \text{Length} \times \text{width} \times 0.75$. Estimated areas of all leaves were summed to obtain total leaf area per plant.

Areas of single leaves, the seventh from top in KDS and ninth leaf in MM and AB, were measured at St. John in each population and each replication. Area of leaves was highly significantly correlated with total leaf area per plant at Manhattan. St. John was considered an additional replication of Manhattan for the purpose of LAI estimation.

Plant and ear height were measured at both locations in Kansas and fifty percent silking and pollination dates were recorded at Manhattan in 1974.

Data were obtained from Kansas and Tlaltizapan, Mexico, in 1974. Tests established at El Batan and Poza Rica, Mexico, were destroyed by an early hail storm and hurricane floods, respectively, before harvest.

Grain yield was obtained from ten guarded plants per plot at both locations in Kansas. Whole plots were harvested at Tlaltizapan after discarding the unguarded plant at the

end of each row. Yields were adjusted to 15.5% moisture and 75% shelling percentage at Tlaltizapan. Grain harvested at the Kansas sites was dried to a uniform moisture level.

All hundred families of each population were screened for specific and wide adaptation. Three synthetics were made for specific adaptation in each population. Each synthetic for specific adaptation was produced by combining ten best families on the basis of yield per plant and yield efficiency at each location. Two synthetics were developed in each population for wide adaptation. Wide adaptation (WA) 1 synthetic hybrids were based on ten best families in each population for yield and YE at all locations. Wide adaptation (WA) 2 synthetic hybrids were based on yield, YE and low coefficient of variation (CV) across locations.

Synthetics were made during winter 1974-75 at Tlaltizapan, Mexico, by bulking pollen from the ten selected families and pollinating the silks with the bulked pollen. Tassels were bagged one day before pollination and silks were covered before emergence to avoid contamination. Seed was harvested from all families in each synthetic and equal weights were bulked. The synthetics are listed in Table 1. Letters K,

Table 1. Populations produced and selection criteria for 1975 evaluation tests

	Population			Selection Criteria
	KDS	MM	AB	
Original	K_0	M_0	A_0	(check)
Manhattan site specific (SS)	K_1	M_1	A_1	Selected for yield/ plant (YP) and yield efficiency (YE)
St. John SS	K_2	M_2	A_2	YP and YE
Tlaltizapan SS	K_3	M_3	A_3	YP and YE
Wide adaptation (WA) 1	K_4	M_4	A_4	YP and YE in all locations
Wide adaptation (WA) 2	K_5	M_5	A_5	YP, YE and low coefficient of variation (CV) across locations
High density (HD)	K_6	M_6	-	YP and YE
Drought Resistance (DR)	K_7	M_7	A_6	Root/shoot ratio in growth chamber

M and A (for KDS, MM and AB, respectively) were used with appropriate subscripts to designate each synthetic.

Synthetics were tested at Manhattan and St. John, Kansas, and Tlaltizapan and Poza Rica, Mexico, in 1975. A randomized complete block design with four replications was used at each location. Each synthetic was planted in four-row plots with 75 cm. between rows and 24 cm between plants.

In addition, K_0 , K_1 , K_4 , K_5 , K_6 , M_0 , M_1 , M_4 , M_5 and M_6 synthetics were tested at Manhattan and St. John at five densities. The K_2 and M_2 site specific synthetics instead of K_1 and M_1 synthetics were used at St. John. Yields in the density trial were obtained by harvesting the whole plot of 2 rows. No corrections for missing hills were made. The trial provided additional environments for estimating stability parameters.

Area of leaves on two plants and area of the seventh leaf from top in KDS and ninth leaf in MM and AB were measured in each plot in the first replication in 1975. Single leaf measurements were made in the other three replications in each population. The appropriate conversion factor, already described, was used for estimating LAI.

Yield data were available from only two Kansas locations during 1975. Severe stunt disease and nutrient deficiency at Tlaltizapan affected the stand of all synthetics. All populations at Poza Rica were severely damaged by downy mildew. Corn leaf blight also reduced yields considerably in all populations.

Grain yields were obtained by harvesting all competitive plants from two central rows in each plot at both Kansas locations. Yield was adjusted to 15.5% moisture.

Estimates of heritability of mean yield and YE over locations in 1974 for 100 families in each population were calculated as follows:

$$\text{Heritability (H)\%} = \frac{s^2_g}{s^2_g + \frac{s^2_{ge}}{l} + \frac{s^2}{rl}} \times 100$$

where s^2_g = genotypic variance component

$\frac{s^2_{ge}}{l}$ = s^2_{ge} = genotype environment (GE) interaction

$\frac{s^2}{rl}$ = variance due to random error

l and r = number of locations and replication per location, respectively

Genotypic and genotype-environment (GE) interaction variance components were calculated to estimate heritability and expected genetic advance under selection for grain yield

and YE across locations in 1974. The following formulae were used for estimating these components from the combined analysis of variance:

$$\sigma^2_g = \frac{MS_1 - MS_2}{r_1} \quad \sigma^2_{ge} = \frac{MS_2 - MS_3}{r}$$

The combined analysis of variance and covariance for grain yield and YE is given in Table 2. Genotypic and phenotypic correlations were estimated between yield and YE for 100 families in each population.

Phenotypic correlations (r_{ph}) were estimated as follows:

$$r_{ph} = \frac{M_{12}}{\sqrt{(M_{11}) \times (M_{22})}} \quad \text{where } M_{12} \text{ is the mean product}$$

for families and M_{11} and M_{22} are the mean squares for families for the characters (yield and YE) under consideration.

The genotypic correlations (r_g) were estimated similarly:

$$r_g = \frac{Cov_{p_{12}}}{\sqrt{(\sigma^2_{p_1}) \times (\sigma^2_{p_2})}} \quad \text{where } Cov_{p_{12}}, \sigma^2_{p_1}, \text{ and } \sigma^2_{p_2}$$

are estimates of progeny covariance component between yield and YE and the progeny variance components of these characters, respectively.

Expected genetic advance in yield and YE from the use of selection indices, expressed in percentage of the change expected when selection was for yield or YE, was calculated in each population. The approach taken was that of Robinson et al. (1951)

Table 2. Form of combined ANOV and covariance analysis for grain yield and YE for randomized block design

Source of Variation	d.f.	Mean Square	Expectation of Mean Square	Composition of Mean Product
Locations (L)	(l-1)			
Replications in locations (R/L)	(r-1)			
Families (F)	(f-1)	MS_1	$\sigma^2 + r\sigma^2_{ge} + rl\sigma^2_g$	$Cov_e + rCov_i + rlCov_f$
Families x Locations (F x L)	(l-1) (f-1)	MS_2	$\sigma^2 + r\sigma^2_{ge}$	$Cov_e + rCov_i$
Error	1(r-1)	MS_3	σ^2	Cov_e

r = number of replications per location

l = number of locations

f = number of families

Cov_e , Cov_i , Cov_f = Covariance of error, interaction, and families, respectively

for estimating genetic advance from a selection index. The formula is:

Expected genetic advance from use of selection index = $\frac{Z}{P} \sqrt{b_1 g_{1Y} + b_2 g_{2Y}}$ where g_{1Y} = estimate of genotypic covariance of YE and yield

g_{2Y} = estimate of genotypic variance of yield

b_1 and b_2 are regression coefficients that give best available weights to YE and yield, respectively.

$\frac{Z}{P}$ = the selection differential in standard units, since 10% superior families were selected so $\frac{Z}{P} = 1.76$

The computation of AOV and regression analysis for evaluating families in each population for stability parameters according to Eberhart and Russell (1966) is presented in Table 3.

Table 3. Analysis of variance and regression analysis when stability parameters are estimated

Source of Variation	d.f.	SS	MS	F
<u>AOV</u>				
Variety	(V-1)	SS_V	$SS_{V/V-1}$	MS_V/MS_{EV}
Environments	(E-1)	SS_{Env}	$SS_{Env/E-1}$	MS_E/MS_{RE}
Reps/Environments	E(R-1)	SS_{RE}	$SS_{RE/E(R-1)}$	MS_{RE}/MS_e
Variety x Environments	(V-1) (E-1)	SS_{VE}	$SS_{VE/(V-1)(E-1)}$	MS_{VE}/MS_e
Regression Analysis				
Variety x Environment	V-1	SS_{VE}	$SS_{VE/(V-1)}$	MS_{VE}/MS_{EV}
V_1	(VR-2)	SS_{EV_1}	$SS_{EV_1/ER-2}$	MS_{EV_1}/MS_e
V_2	(VR-2)	SS_{EV_2}	$SS_{EV_2/(ER-2)}$	MS_{EV_2}/MS_e
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
V_v	(VR-2)	SS_{EV_v}	$SS_{EV_v/(ER-2)}$	MS_{EV_v}/MS_e
Pooled Environment Deviation	(V-1)(VR-2)	SS_{EV}	$SS_{EV/(V-1)(VR-2)}$	MS_{EV}/MS_e
Error	edf*	SS_e	SS_e/edf	

* $edf = VER - ((V-1) + (E-1) + (E(R-1) + (V-1)(E-1))$

RESULTS

Results of the progeny test, estimate of heritability and genetic advance of the three populations tested in 1974 at three locations are presented in Table 4. Mean yield and yield efficiency (YE) were highest for KDS and lowest for MM at Manhattan, Kansas. Amarillo Bajio and MM had higher yield and YE than KDS at Tlaltizapan, Mexico. Yields across locations were highest for AB followed by KDS and MM. However, KDS had highest mean YE at three locations.

Heritability estimates for grain yield and YE were highest for MM and lowest for KDS. The estimates for full-sib families of AB might be biased due to presence of non-additive variance component. The predicted genetic advance was greatest for AB and MM.

Analyses of variance for yield for 100 families of each population at each location is presented in Table 5. Significant differences for yield in half-sib families of KDS occurred at St. John and Tlaltizapan; differences were insignificant at Manhattan. Half-sib families of MM differed significantly at all locations. Yield differences among full-sib families of AB were significant only at Manhattan and St. John.

Table 4. Mean yield and yield efficiency of 100 families of three corn populations, estimates of heritability and genetic advance under selection for grain yield at three locations during 1974

Location	KDS		Mex Mix		Amarillo Bajio	
	Yield	Y.E.	Yield	Y.E.	Yield	Y.E.
	kg/ha	g/m ²	kg/ha	g/m ²	kg/ha	g/m ²
Manhattan	5590	166	4070	91	5230	107
St. John	7120	213	5640	122	7710	156
Tlaltizapan	5410	189	7050	197	8710	224
Mean	6040	189	5590	136	7210	162
Herita- bility %	4.69	27.66	40.59	34.12	22.04	34.95
Genetic Advance (kg/ha)	9.84	-	301.52	-	411.74	-

Table 5. Mean squares for grain yield of 100 half-sib families of KDS and MM and 100 full-sib families at each of three locations during 1974

	d.f.	KDS			MM			AB		
		Man.	St.J.	Tlalt.	Man.	St.J.	Tlalt.	Man.	St.J.	Tlalt.
Replication	1	2.39	9.36	5.27	19.49	266.02	0.005	12.47	5.50	11.36
Families	99	1.10	3.99*	2.25*	1.40*	78.55**	1.53*	1.52*	1.52*	1.45ns
Error	99	1.31	2.78	1.56	0.94	28.49	0.99	1.03	1.26	1.55

** significant at 1% level of probability
 * significant at 5% level of probability
 ns not significant

Mean squares from combined analysis of variance of yield and yield efficiency in three locations for 100 families of each population are shown in Table 6. Highly significant differences for yield occurred in KDS and MM. Differences in yield of AB families across locations were not significant. Yield efficiency of MM, unlike KDS, differed significantly at 0.01 level of probability, suggesting greater genetic variability.

Family x location interactions were highly significant for yield and YE in KDS and MM, but were significant only for YE in AB.

Components of variance for genotype and genotype-environmental interactions for yield and YE in each population over three locations are given in Table 7. Both components of variance were significant for yield and YE at 1% level of probability in MM, insignificant for yield in AB, but significant for YE in AB and KDS. Genetic variance components for yield in KDS were not significant, but the interaction components were highly significant. These variance components for KDS, MM and AB appeared to be biased from the presence of genotype-environment interactions.

Phenotypic (r_{ph}) and genotypic (r_g) correlations between yield and YE for 100 families in each population were estimated across locations. Positive and highly significant estimates

Table 6. Mean squares for 100 Families of KDS, MM and AB in combined analysis of variance for yield and YE across locations during 1974

Source	d.f.	KDS		Mex Mix		AB	
		Yield	YE	Yield	YE	Yield	YE
Locations	2	175.56	100156.68	444.45	597404.84	640.95	687334.92
Replication/ Location	3	2.53	11109.32	9.37	4294.51	10.92	13208.68
Families	99	1.81**	2140.39ns	2.63**	2177.19**	1.675ns	1074.48ns
Families x Location	198	1.73**	1995.46**	1.56**	1369.67**	1.31ns	867.48*
Error	297	1.15	1236.81	0.96	739.62	1.127	680.67

** significant at 1% level of probability
 * significant at 5% level of probability

ns not significant

Table 7. Genotype and genotype-environment interaction variance components for grain yield and yield efficiency for three populations of corn across locations during 1974

Population	Yield (kg/ha)		Y.E. (gram/m ²)	
	σ^2_g	σ^2_{ge}	σ^2_g	σ^2_{ge}
KDS	14194.06 ns	288009.80**	111.71*	240.82*
Mex-Mix	178120.00**	301012.73**	123.37**	352.67**
AB	61493.87 ns	89158.68 ns	71.49**	38.81*

*, ** significant at the 0.05 and 0.01 level of probability, respectively

ns not significant

were obtained for MM ($r_{ph} = 0.885, **$ $r_g = 0.939**$) and AB ($r_{ph} = 0.719, **$ $r_g = 0.718**$). Phenotypic correlations for KDS were insignificant and negative ($r_{ph} = -0.071$ ns, $r_g = 0.711**$) This non-correspondence of the phenotypic and genotypic correlations was likely caused by large genotype-environment interactions.

Phenotypic variances and covariances used to form correlation coefficients between yield and YE provided the basis for constructing indices. The indices are shown in Table 8. Expected gains in yield or YE of AB and MM were small when the selection index was based on yield and YE but expected gains for yield or YE were relatively large in KDS.

Stability parameters, mean regression coefficients ($\bar{b}$) and mean square deviations from regression (S^2_d) for 100 families in each population at three locations were calculated according to Eberhart and Russell (1966) and are presented in Table 9. Populations KDS and AB appeared more desirable because of their high mean yield and favorable $\bar{b}$ value, although mean S^2_d was large for all populations. Mean $\bar{b}$ and S^2_d were similar in MM and AB; MM had relatively low mean yield and higher standard deviation than either KDS or AB. Large S^2_d values for each population were probably caused by lack of experimental data from additional environments. The

Table 8. Progress expected in yield and yield efficiency from selection based on a combination of characters. Progress expressed as percentage of the expected when selection was for yield or yield efficiency at three locations

Character	Population		
	KDS	MM	AB
1. Selecting for yield		%	
Yield + LAI	171	102	105
Yield + YE	160	100	103
Yield + LAI + YE	164	100	104
2. Selecting for YE			
YE + Yield	147	106	114
YE + LAI	145	104	102
YE + Yield + LAI	148	116	112

Table 9. Stability parameters ($\bar{b}$ and $\bar{S}_d^2$) for yield of 100 families in each population in three locations during 1974

Population	Regression Coefficient	Standard Deviation	Squared Deviation	Mean Yield
	$\bar{b}$	$\bar{S}_D$	$\bar{S}_d^2$	kg/ha
KDS	1.000	404	576000**	6040
Mex Mix	0.999	728	70800**	5590
AB	0.999	324	667000**	7210

** significant at 0.01 level of probability

stability parameter, (S^2_d), requires relatively many environments for valid results.

Mean squares from analysis of variance for estimating genetic differences in regression on environmental index among families of the populations were calculated. The analyses in Table 10 show that mean squares for family x location (linear) were significant for only YE in MM ($P=0.01$) and for yield in AB ($P=0.10$). The analyses indicated that families in KDS failed to respond linearly across environments for yield or YE.

New synthetics developed during 1974-75 at Tlaltizapan, Mexico, were tested for performance in 1975. Yield per plant and YE of all synthetics from three populations at Manhattan and St. John and average of the two locations are presented in Tables 12, 13 and 14. No significant differences in yield between original population and new synthetics of KDS and AB occurred at any location. This might be caused by the effect of combined selection criteria of yield per plant and YE, which increased LAI of the new synthetics. Increased LAI was not associated with increased yield. Significant differences ($P=0.05$) in YE of some synthetics of KDS and AB occurred at Manhattan. Yield efficiency was higher in the original populations than in the new synthetics of both populations.

Significantly larger leaf area developed by the synthetics than by the original populations resulted in lower

Table 10. Mean square from analysis for stability parameters in 100 families of each population during 1974.

Source	d.f.	KDS		MM		AB	
		Yield (tons/ha)	YE	Yield (tons/ha)	YE	Yield (tons/ha)	YE
Location (linear)	1	351.0	197896.1	888.9	191419.5	1281.8	373978.6
Family x Location (linear)	99	1.86	1034.22	1.45	2025.4**	¹ ✓ 1.35	833.07
Pooled deviations	100	1.57	2446.99	1.66	824.8	1.24	755.60
Pooled Error	297	1.153	1271.32	0.96	723.96	1.127	720.539

¹✓ significant at 0.10 level of probability

** significant at 0.01 level of probability

Table 11. Mean leaf area index (LAI) for synthetics in three corn populations at two locations during 1975

Synthetics	Manhattan	St. John
	LAI	
K ₀	3.23	3.46
K ₁	4.15	3.66
K ₂	4.20	3.75
K ₃	4.40	3.68
K ₄	4.12	3.79
K ₅	3.91	4.17
LDS .05	0.36	ns
M ₀	5.21	3.65
M ₁	5.17	3.65
M ₂	5.68	4.16
M ₃	5.59	4.37
M ₄	4.96	4.50
M ₅	5.12	3.97
LSD .05	ns	0.45
A ₀	4.35	4.71
A ₁	5.51	4.43
A ₂	5.85	4.58
A ₃	4.67	4.62
A ₄	4.52	4.31
A ₅	4.83	5.05
LSD .05	0.53	0.42

Table 12. Mean yield and mean yield efficiency of KDS synthetics at Manhattan and St. John during 1975

Synthet- ics	Manhattan		St. John		Combined Locations	
	Yield	YE	Yield	YE	Yield	YE
	g/plant	g/m ²	g/plant	g/m ²	g/plant	g/m ²
K ₀	118.98	202.83	116.35	190.14	117.66	196.48
K ₁	134.48	179.67	113.92	173.05	124.20	176.36
K ₂	113.03	150.62	96.72	143.19	104.88	146.90
K ₃	131.98	166.20	118.80	178.48	125.39	172.34
K ₄	117.48	158.73	123.02	180.50	120.25	169.62
K ₅	118.03	167.67	103.50	138.11	110.76	152.89
K ₆	114.18	130.44	115.65	169.29	114.91	149.86
K ₇	119.18	168.09	114.42	182.37	116.80	175.23
LSD 0.05	ns	31.43	ns	ns	ns	30.97

Table 13. Mean yield and mean yield efficiency of Mex Mix synthetics at Manhattan and St. John during 1975

Synthet- ics	Manhattan		St. John		Combined Locations	
	Yield	YE	Yield	YE	Yield	YE
	g/plant	g/m ²	g/plant	g/m ²	g/plant	g/m ²
M ₀	84.37	89.63	50.67	76.32	67.53	82.98
M ₁	103.10	110.91	77.67	115.58	89.14	113.25
M ₂	75.52	74.23	55.02	73.07	65.28	73.65
M ₃	77.22	76.78	67.70	85.84	72.48	81.31
M ₄	109.55	122.48	79.40	97.81	94.48	110.14
M ₅	101.72	109.99	72.80	101.21	87.26	105.60
M ₆	101.82	118.78	63.27	74.13	82.55	96.46
M ₇	82.30	86.04	55.32	61.66	68.81	77.42
LSD 0.05	13.66	20.71	ns	23.49	20.44	21.45

Table 14. Mean yield and mean yield efficiency of AB synthetic at Manhattan and St. John during 1975

Synthetics	Manhattan		St. John		Combined Locations	
	Mean yield g/plant	YE g/m ²	Mean yield g/plant	YE g/m ²	Mean yield g/plant	YE g/m ²
A ₀	114.27	145.51	113.27	113.04	113.78	139.28
A ₁	108.40	110.68	95.92	119.27	102.16	114.98
A ₂	111.77	106.09	112.27	135.77	112.03	120.93
A ₃	108.75	128.38	99.45	118.76	104.10	123.57
A ₄	119.87	148.65	102.17	131.41	111.03	140.03
A ₅	114.55	131.48	127.12	139.30	120.84	135.39
A ₆	109.20	94.43	103.20	115.63	106.20	105.03
LSD 0.05	ns	35.53	ns	ns	ns	ns

YE (Table 11). New synthetics in both populations also had lower YE than their respective original populations at St. John, but differences were not significant at the 5% level. Large LAI in these synthetics was likely caused by more weight given to yield per plant than to YE during selection of the best families for each synthetic.

In MM, the Manhattan site specific (M_1) and wide adaptation (M_4 and M_5) synthetics had significantly higher yield and YE than the original population, M_0 , at Manhattan. Relative greater progress from one cycle of selection in some synthetics of this population was probably caused by large genetic variability for yield and YE. No yield and YE differences among M_0 , M_2 and M_3 at Manhattan were expected because these synthetics were selected for specific adaptation at locations other than Manhattan. Yield did not differ at St. John between synthetics, but YE was significantly higher for M_1 and M_5 than for M_0 . Yield did not differ for M_0 and M_2 (St. John site specific) because the ten best families were not used to form the synthetic M_2 . Synthetic M_2 was expected to yield equal to or less than M_0 at that site because the families were selected randomly.

The combined analysis of variance for yield of KDS and AB synthetics at the locations indicated no significant

differences, whereas, in MM yield of M_4 was significantly superior to M_0 (Table 15). Thus, the combined selection (YP and YE) criteria were successful in a highly variable population in which slightly increased LAI did not concurrently decrease yield or YE. Non-response or negative response to selection for yield or YE in more homogeneous populations, KDS and AB, might have occurred from selection that was not based on best available weights of YP and YE. Some progress might have occurred in one cycle of selection if proper weights of YP, YE and LAI were applied.

There was no evidence of lack of genetic variance components in any population, and genotypic variance components were significant in all populations in 1975 performance tests (MM $\sigma^2_g = 336905.12^{**}$ and $\sigma^2_{ge} = 25387.02$ ns, KDS $\sigma^2_g = 74533.30^{**}$, $\sigma^2_{ge} = 12355.75$ ns).

The MM density study provided additional environments for estimating stability parameters in M_4 , M_5 and M_0 (Table 16). Synthetic M_4 was superior to M_0 in all environments, while M_5 was equal or slightly better than M_0 in these environments. Selection criteria for M_5 for low coefficient of variation in addition to YP and YE might have resulted in less stability compared to M_4 .

Table 15. Combined analysis of variance of yield of KDS, Mex Mix and Amarillo Bajio for 2 locations during 1975

Source	d.f.	KDS	Mex Mix	d.f.	Amarillo Bajio
		MS			MS
Location	1	1053.00	11691.02	1	318.73
Replication/ Location	6	137.66	200.94	6	591.73
Synthetics	7	369.54 ns	7097.28**	6	330.04 ns
M_0 vs M_4	1	-	726.30*		-
	6	-	1061.83**		-
Synthetics x Location	7	173.85 ns	154.40 ns	6	197.14 ns
Error	48	157.63	121.02	42	439.90

*, ** Significant at 0.05 and 0.01 level, respectively

ns Not significant

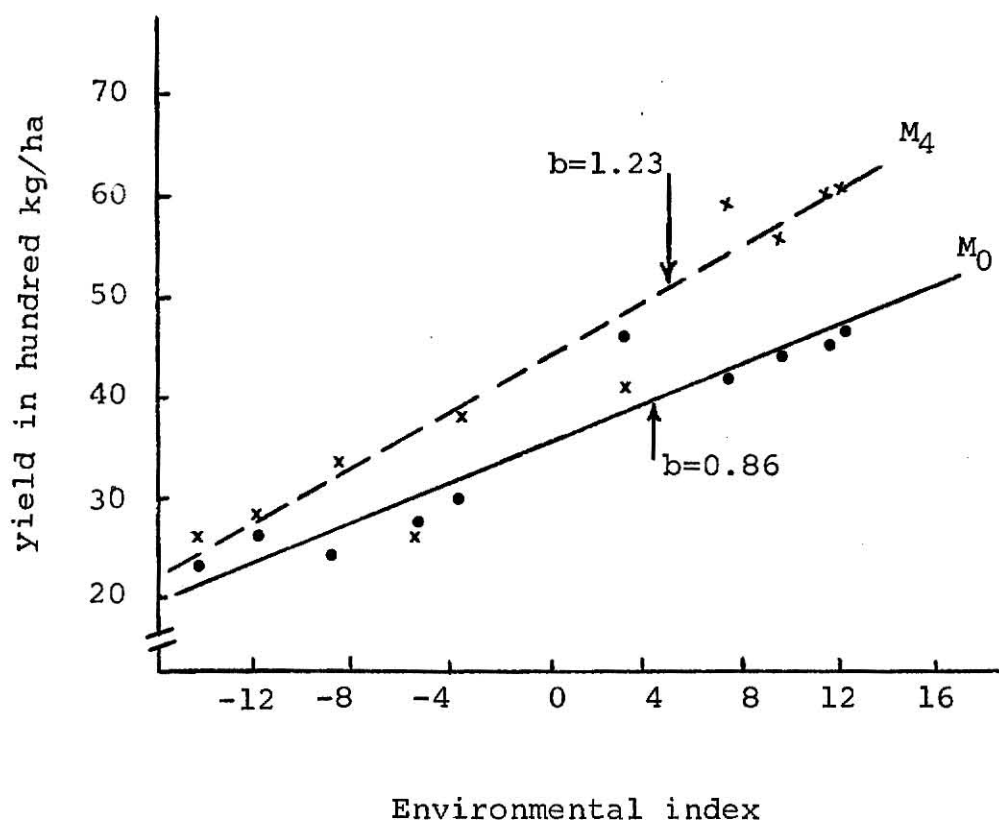
Table 16. Regression coefficients and deviation mean squares when stability parameters are estimated

Source	Regression Coefficient (b)	Deviation Mean Square
Synthetics x Environment (linear)		4691797.80**
Synthetic M_0	0.9	547601.38
Synthetic M_4	1.2	581782.70
Synthetic M_5	1.0	428308.57
Synthetic M_6	0.9	631957.87
Pooled Environment Deviation		729883.51 *
Error		511785.75

*, ** significant at the 5% and 1% level, respectively

Figure 1 illustrates differences in stability and performance of M_4 (wide adaptation) and M_0 (original) in varying environments. Synthetic M_4 is desirable because its performance was uniformly superior ($b = 1.23$ and $\bar{x} = 107\%$ of $\bar{x}$). In contrast, M_0 was uniformly lower in performance in all environments ($b = 0.86$ and $\bar{x} = 87\%$ of $\bar{x}$).

Fig. 1 Response of two synthetics, M_4 (wide adaptation) and M_0 (original) to varying environments.



DISCUSSION

Genetic potential was higher in the AB population than either the KDS or MM population, as measured by the mean performance of the populations across locations. Mex-Mix, which apparently was more adapted to a tropical environment, had greater leaf area, lower yield and low YE in the temperate Kansas environments. This was probably caused by photoperiod sensitivity of MM. Francis et al. (1970) observed sensitivity to photoperiod in corn genotypes adapted to tropical regions.

Magnitude of genotypic and genotype-environment interactions for yield and yield efficiency varied considerably in the three populations. The larger genetic variance component for MM than for AB or KDS, although error mean squares were similar for the three populations, agreed with results of Goodman (1965). He reported larger genetic estimates for corn composites of more diverse origin than for composites of less diverse populations. Significant genotype-environment interactions among the families in each population indicated differences in adaptation. The large genotype-environment interactions might have affected the variance components in AB and KDS. The large interactions might also have been a source of random errors of variance estimates and probably introduced upward biases (Otsuka

et al., 1972; Stuber et al., 1973). Lonnquist (1967) thought that unbiased variance estimates from experiments over one or even more locations or years are limited.

Heritability estimates also seemed to be somewhat biased in all populations, particularly in full-sib families of AB, because of possible non-additive variance component.

Highly significant positive correlations between yield and YE indicated strong positive association between the two characters in all three populations except KDS. The non-correspondence of correlations in some cases is not unusual and may be attributed to large genotype-environment interaction.

Expected gains in yield of AB and MM were small when the selection index was based on yield and YE, but were relatively larger when the selection index was based on yield, YE and LAI. This indicated that LAI was an important trait to be considered during selection.

Stability parameters, mean yield, mean regression coefficient (b) and deviation from regression (S^2_d), defined by Eberhart and Russell (1966), for stability of performance in a series of environments, were desirable for AB and KDS. However, S^2_d was greater than desirable in all populations. Significant S^2_d resulted from a variety trial of limited number of environments. Eberhart and Russell (1966) recommended several environments with minimum replications per environment for

obtaining reliable estimates of S^2_d . Tai (1971) compared genotypic stability results of a potato experiment with eight genotypes and six environments with phenotypic stability results of Eberhart and Russell. Estimates obtained from the two methods differed very little.

Family x environments (linear) sums of squares on environmental index from analysis of variance for stability indicated non-linear response for yield and YE in all populations except YE in MM. The non-linear response was likely caused by the small number of environments. However, family x environment (linear) response was significant for yield in AB at the 0.10 probability level. This result agreed with those of Eberhart and Russell (1966) and Perkins and Jinks (1968). They found that genotype-environmental interactions in performance trials in a series of environments were linear or nearly linear.

Grain yield did not differ between new synthetics and their original populations or among the new synthetics at Manhattan and St. John except MM. The significantly larger LAI developed by new synthetics than by the original KDS population at Manhattan was probably caused by combined selection criteria of YP and YE. Selection gave more weight to yield per plant than to YE and caused significantly larger LAI in KDS at Manhattan and in AB at both locations. This correspondingly

decreased YE of KDS and AB and resulted in insignificant differences in yield at both locations. Muleba and Paulsen (1976) and Tanaka and Yamaguchi (1972) reported negative relationship between LAI and YE in experiments with corn. Large LAI did not correspond with larger yield or YE. At Manhattan, larger LAI contributed negatively to YE of KDS and AB in which original populations had significantly higher YE than their new synthetics.

However, higher yield and YE of M_4 (WAI) and M_1 (Manhattan SS) over the original and other MM synthetics at Manhattan indicated progress from selection. Similarly, M_1 , M_4 and M_5 had significantly higher YE than M_0 , M_2 and M_3 at St. John, although no significant differences for yield occurred there.

Selection was probably effective in MM, apparently because its high genetic variability was conducive to improvement in a single cycle of selection. Also, proper weights of yield and YE appeared to be important in selection. The combined selection criteria of yield and YE did not increase LAI correspondingly as it did in the other populations. The effect of selection criteria seemed to be affected by the structure of the populations. Yield and YE increased in MM, but LAI increased only slightly at Manhattan and increased significantly more in some new synthetics than in the original population at

St. John. Synthetics of MM that developed larger LAI did not always yield higher. However, combined selection criteria of yield and YE appeared to be detrimental to yield or YE in the more homogeneous populations, KDS and AB.

Analysis of synthetics M_0 , M_4 and M_5 in density trials according to Eberhart and Russell (1966) indicated more stability of M_4 (WAI) than M_0 . Synthetic M_4 was uniformly superior across environments with acceptable stability parameters b and S^2_d . Synthetic M_5 was only slightly better than M_0 in some environments, indicating that selection criteria of low coefficient of variation in addition to yield and YE for M_5 (WA2) resulted in less stability compared to M_4 .

Selection for yield or YE alone would have increased yield or YE more than was the case with combined selection criteria. If several traits such as yield and YE, etc. are to be combined into one plant type, then accurate estimates of genetic variability, genetic correlations, and heritabilities for these traits are needed.

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SELECTION FOR WIDE AND SPECIFIC ADAPTATION
IN THREE POPULATIONS OF CORN (ZEA MAYS L.)

by

MOHAMMAD SALIM KHAN

B.Sc. (Hons), University of Peshawar, Pakistan, 1965

AN ABSTRACT OF A MASTER'S THESIS

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KANSAS STATE UNIVERSITY
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One-hundred families in each of three populations of corn (Zea mays L.) - Kansas drought synthetic (KDS), Mex-Mix (MM) and Amarillo Bajio (AB) - were tested for wide and specific adaptation at Manhattan and St. John, Kansas, and Tlaltizapan, Mexico, during 1974. The ten best families in each population were combined into synthetics for specific adaptation at each location and into synthetics for wide adaptation at all locations. Selection criteria were yield per plant (YP) and grain yield per unit of leaf area (yield efficiency, YE) for each specific adaptation and wide adaptation synthetic, and YP, YE and a low coefficient of variability for a second set of wide adaptation synthetics. New synthetics were tested against original populations at the two Kansas sites during 1975.

The combined selection criteria of YP and YE increased LAI indirectly and caused non-significant differences for yield between original and new synthetics of KDS and AB. Larger LAI in new synthetics also caused lower YE in KDS and AB. However, selection criteria were more effective in the Mex-Mix population. Manhattan site specific adaptation (M_1) and wide adaptation (WA)1 Mex-Mix synthetics were superior to the original population in yield and YE at Manhattan. The wide adaptation synthetic exhibited more stability for yield than the wide adaptation synthetic selected for a low coefficient

of variation when the synthetics were tested in a series of environments.

Highly significant positive genotypic correlations between YP and YE occurred in all three populations. Genetic variability and heritability estimates for yield over three environments were higher for MM than for AB and KDS. Heritability estimates for YE were similar for MM and AB, but were slightly lower for KDS. Large genotype-environment interactions likely affected reliability of heritability estimates.