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A Comprehensive Breeding System*

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Summary. An outline of a comprehensive breeding system developed and used by the Kenya Maize Research Section is presented. This system has four main phases:

1. Evaluation of local and exotic varieties so that the breeding material is the best available.

2. Compositing the selected breeding material into two or more populations or varieties in such a manner that each population has considerable genetic variation for the traits requiring improvement and that the crosses of these populations will show heterosis.

3. Recurrent selection in each population to increase the frequency of favorable genes so that the populations and population crosses are improved with each cycle of selection.

4. Release of a commercial variety of one of the following forms: (a) the cross of two populations as a variety cross hybrid; (b) single, three-way or double cross hybrids from inbred lines developed from the elite material after each cycle of selection; or (c) a synthetic variety derived from the advanced generation of the population cross in areas where hybrid production is not yet feasible.

Preliminary results are presented to indicate the improvement possible in maize by use of this system. Its possible extension to other crops is also briefly discussed.

* Dedicated to Dr. GEORGE F. SPRAGUE on the occasion of his 65th birthday.

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Many new breeding programs are being established in the research programs of the developing countries as well as within established programs elsewhere to produce improved varieties for specific ecological conditions. If leaders of these new projects plan their work systematically and make use of recent developments in breeding methods, better varieties can be produced more quickly with a smaller expenditure of funds and manpower.

Such a comprehensive breeding system has been developed for maize improvement by the Maize Research Section, Kitale, Kenya. This paper presents a brief outline of the system for consideration by other breeders for developing not only improved maize varieties, but also improved varieties of other crops.

Breeding Material

The selection of superior breeding material is, of course, the first step. Two or three years spent introducing and evaluating exotic material in addition to the local varieties can often produce greater increases in mean performance than a ten-year breeding program which utilizes only the readily available local material. Another important aspect is the increased genetic variation normally produced when material of diverse origin is introduced and combined into breeding populations.

The systematic introduction of improved varieties is especially important in areas where the crop is not indigenous. Improved synthetic varieties and hybrids from similar ecological conditions are the most desirable accessions although all types of material can be utilized. Material from extremes can often be useful in an intermediate area. For instance, a cross between an early maturing, high altitude variety and a late maturing, coastal variety may give good performance and combining ability for areas of intermediate altitudes.

The large number of local collections and introductions available requires a large evaluation program. Since general combining ability is most important in the preliminary screening, the comparison of all collections as testcrosses to a local variety is often the most satisfactory method of evaluation. The testcross seed can be obtained easily for maize by growing the collections in isolation, using the tester as pollen parent and detasselling the collections. Notes on various agronomic characters can be recorded in this testcross seed production plot. The following season, yield trials to evaluate the testcrosses should be grown with few replications at several locations throughout the area. COMSTOCK and MOLL (1963) suggest that one season's results will usually provide adequate information from which to select the best entries if enough locations are used.

Compositing Breeding Populations

The final goal is to develop two breeding populations (Variety A and Variety B) that give considerable heterosis when crossed and yet have adequate genetic variation within each population to permit rapid progress from recurrent selection. The variety cross hybrid ($A \times B$) will be higher yielding than any single synthetic; and double crosses with a parental single cross from each population tend to yield higher than if the parental single crosses come from the same population. The inbreeding which results from recurrent selection in populations of finite size is eliminated by using the variety cross or advanced generations of the variety cross.

The use of two populations gives increased flexibility to the breeding program. If hybrids are not feasible as a commercial product at this stage because of production or marketing problems, the advanced generation of the variety cross may be sold as a synthetic variety. If progress from recurrent selection is so rapid that the variety cross from the current cycle of selection is superior to current double cross hybrids of inbred lines from previous cycles of selection, the variety cross hybrid can be used commercially. If the market demands uniform hybrids, or if overdominance or over-dominant types of epistatic gene action become important as the additive variance is exhausted, the best lines from each cycle of selection can be inbred further and tested in hybrid combination. Because of the known heterosis between varieties A and B, only $A_i \times B_m$ type single crosses or $(A_i \times A_j)\ (B_m \times B_n)$ type double crosses need be evaluated, where A_i and A_j lines come from Variety A, and B_m and B_n lines come from Variety B.

When the parental varieties (in HARDY-WEINBERG equilibrium) and a diallel of all possible variety crosses are grown, the mean of a population composited from any combination of varieties can be predicted as follows if epistatic effects are negligible:

$$\text{Composite} = \overline{VC} - \left(\frac{\overline{VC} - \overline{V}}{n}\right)$$

where $\overline{V}$ is the mean of the varieties going into the composite, n is the number of varieties and $\overline{VC}$ is the mean of all variety crosses from these varieties. If varieties M_1 to M_m are composited into A and varieties N_1 to N_n are composited into variety B, the variety cross ($A \times B$) can be predicted as follows:

$$A \times B = \frac{1}{mn}(M_1 N_1 + M_1 N_2 + \cdots + M_1 N_n + \\ + M_2 N_1 + \cdots + M_m N_n)\,.$$

The diallel gives no information on the genetic variance within the composited varieties, but additive genetic variance is greatest at intermediate gene frequencies. Since the gene frequency for each locus in a composited population is the average frequency from the varieties going into the population, gene frequencies for many loci will tend to be intermediate values. Therefore, the genetic variance should be increased by compositing diverse varieties.

A modification of plant-row selection proposed by LONNQUIST (1964) can be used to ensure thorough recombination while the entries are being composited and yet permit elimination of the less desirable material. In this method, the entries are planted in a replicated yield trial and detasselled. Rows of bulked seed of all entries are planted between ranges of the yield trials to provide pollen. At harvest the best ears within each entry are saved and bulked over replications to represent that entry in the following season. The individual entries are planted in a similar manner for at least four generations. As recombination progresses, the variation among entries will decrease until a uniform composite or synthetic

variety is produced. Intense selection at a level of 5–10% can be carried out in the first cycle while each entry is pure; but the intensity should be reduced to 25–50% in the second and third cycles when the "entries" are mixtures of variety crosses. Thereafter the selection intensity can be gradually increased again. The total number of ears saved in each cycle from all entries should be fairly large, perhaps 800–1,000, to prevent loss of favorable genes due to finite population size.

Population Improvement

Recurrent selection has been shown to be effective in increasing yield as well as in improving the more highly heritable agronomic characters (MOLL and ROBINSON 1966, PENNY et al. 1963, SPRAGUE 1955, SPRAGUE et al. 1959). Many methods of selection have been proposed and used. The particular method that is to be used for a breeding program should be selected on the basis of the experience and training of the personnel, the facilities and funds available and the variation, both genetic and environmental, in the material under selection.

Mass selection (GARDNER 1961, LONNQUIST et al. 1966, WILLIAMS and WELTON 1915) and plant-row selection (LONNQUIST, 1964) require no hand pollinations. Mass selection has a small land requirement but normally will not progress as rapidly as some form of progeny testing at several locations. Both of these methods require isolation to prevent contamination of the selected material by local maize.

With reference to SPRAGUE's outline for recurrent selection for general combining ability (SPRAGUE 1952, 1955, 1966), RAWLINGS and THOMPSON (1962) have pointed out that a tester with low gene frequencies of favorable alleles is most desirable as a tester for loci showing partial to complete dominance. A low yielding tester selected from the same population should then be an excellent tester; but this means doubling the selection work until the tester has been developed. Reciprocal recurrent selection (*RRS*) (COMSTOCK et al. 1949) is effective for loci showing over-dominance or over-dominance types of epistasis. However, most data suggest that partial to complete dominance may be more important (MOLL et al. 1964, 1966, PENNY et al. 1963, SPRAGUE et al. 1959). As progress from selection increases the frequencies for favorable genes, reciprocal recurrent selection becomes less efficient for these latter loci. S_1 testing *per se* appears theoretically to be a useful method since the variability among lines is increased by inbreeding (COCKERHAM 1963, SPRAGUE 1966, SPRAGUE et al. 1952).

Formulas for expected gain from selection (SPRAGUE 1966) provide a basis for comparing expected rates of progress if estimates of variance components are available. Obtaining these estimates from mass selection and half-sib family selection trials during the initial selection program is preferable to spending time and money on separate experiments while selection is delayed. Plant-row selection as proposed by LONNQUIST (1964) involves half-sib family selection. However, since no control of the male parent is exercised, progress from selection is only half that of half-sib family selection and recombination of remnant seed. This can be improved by eliminating undesirable pollen parents before tasselling and by mass selection within the plant-row trial in isolation when the maternal plants are selected for the subsequent cycle.

Expected gain should be expressed as gain per year for fair comparisons of the various methods. Mass selection and plant-row selection are relatively efficient if full-sib selection and S_1 testing *per se* require two and three years, respectively. However, if off-season nurseries permit these latter methods to be completed in a year, progress per year is normally much slower by mass selection and plant-row selection.

Most recurrent selection in maize has been for a single attribute. Index selection has been proposed when several characters must be improved simultaneously (BRIM et al. 1961, HAZEL 1943). Estimation of the necessary genetic variances and covariances, however, is expensive and time-consuming unless it is done from selection trials. Index selection should be done in the nursery as well as in yield trials. Most agronomic characters are highly heritable and will respond to phenotypic selection. Therefore, as an alternative to index selection, phenotypic selection for the agronomic characters can be done in the nursery during recombination and the preparation of material for yield trials; and selection of entries in yield trials can be based on yield alone. In mass selection trials the detasselling of agronomically undesirable plants prior to pollen shed should also be effective in improving other traits while still keeping the main emphasis on yield improvement. In plant-row selection trials the elimination of undesirable male plants can provide the selection pressure for agronomic traits so that selection among and within plant rows can be made exclusively for yield.

Results

The improvement program for late maturing maize varieties began at Kitale in 1955 with the collection and evaluation of local farmer's strains. Since the Kitale Agricultural Station strain was one of the best local varieties, recurrent selection for general combining ability was initiated using the method of half-sib family selection and recombination of remnant S_1 seed. Each cycle required five years but steady progress was obtained (Table 1). S_3 lines were selected from the top lines used in forming Kitale II and Kitale III, and these lines were evaluated in single, three-way, and double cross combinations. The best of these conventional hybrids were designated Hybrids 621, 631, 622 and 632, and were released for commercial use.

Table 1. *Performance of Kitale Station maize and improved selections grown at nine locations in 1965.*

Variety	Cycle of Selection	Mean Yield	
		100 kg/ha	%
Kitale Station	C_0	38.7	100
Kitale II	C_1	40.1	104
Kitale III	C_2	44.0	114

In the next stage a large collection of Central and South American material was obtained in 1959 from the Rockefeller Foundation, and these were test

Table 2. *Mean yields of Kenya varieties from 14 locations in 1965 and 20 locations in 1966.*

Variety	Hybrid Pedigrees	Year of Release	Mean Yields	
			100 kg/ha	%
Kitale II		1960	43.2	100
Kitale III		1965	—	107*
Hybrid 611	(Kitale II × Ec.573)	1964	—	120*
Hybrid 611B	(Kitale III × Ec.573)	1966	56.8	131
Hybrid 621	(*A* × *G*) (*D* × *E*)	1964	—	124*
Hybrid 622	(*A* × *F*) (*G* × *D*)	1965	53.4	124
Hybrid 632	(*A* × *G*) *F*	1965	56.5	131
Hybrid 612	(*A* × *G*) Ec. 573	1965	56.8	131
Hybrid 613B	(*F* × *G*) Ec. 573	1966	—	143**
L.S.D. (.05)			3.5	

* Data available for 1965 only. — ** Data available for 1966 only.

crossed to Kitale II and evaluated. Three of the best accessions were found to be Ecuador 573 (Ec. 573), Costa Rica 76, and Cometico. The variety-cross (Kitale II × Ec. 573) was so outstanding, especially at higher altitudes, that seed of Ec. 573 was increased and the variety-cross was released as Hybrid 611 in 1964.

The relative yields obtained in district trials of synthetic and both types of hybrid varieties are shown in Table 2 and expressed diagrammatically in Figure 1. Although ten years were required to produce the conventional hybrids, only five years and far less selection work were required for H611. By introducing the adapted exotic variety Ec. 573, higher yields were obtained above 1800 meters from the variety cross hybrid than from inbreeding and hybridization in local varieties. The improvement from Kitale Station maize to Kitale III was not wasted as the improvement is carried through into the varietal hybrid, e.g., Kitale III × Ec. 573 (H611B) outyielded Kitale II × Ec. 573 (H611) by 11%.

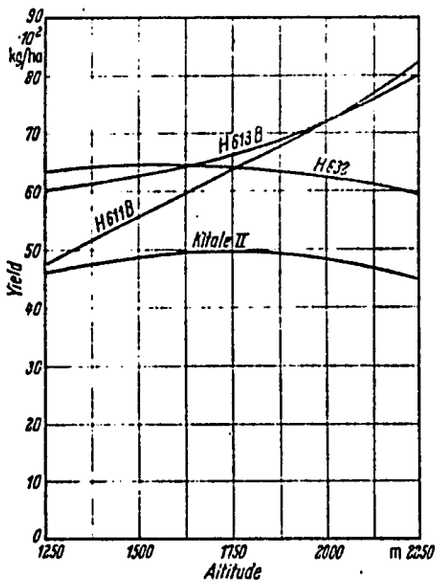

Fig. 1. Response of Kenya varieties to varying elevations in 1966 for 20 locations.

The long range breeding program is now based on Kitale Composite *B*, Kitale Composite *C* and Kitale Composite *E*. Kitale Composite *B* was formed from the superior local varieties and selections from these, including the single crosses of the elite inbred lines derived from these varieties. Kitale Composite *C* was formed by compositing selections from Ec. 573, Costa Rica 76 and Cometico. Many of the Central American accessions had desirable agronomic characters but were lower in yield than selections composited in Kitale Composite *C*. Hence, a third, more widely-based variety (Kitale Composite *E*) was composited to include: (a) these other entries, (b) all entries included in Kitale Composite *B*, and (c) all entries included in Kitale Composite *C*.

The improvements made in Kitale Composites *C* and *E* by the method described in the previous section are impressive (Table 3). Kitale Composite *E* approaches

Table 3. *Mean yields of Kenya composite varieties and variety crosses from 10 locations in 1966.*

Variety	Mean Yield	
	100 kg/ha	%
Kitale II	50.9	100
Ec. 573	38.7	76
Kitale Composite *A*	51.2	101
Kitale Composite B	54.1	106
Kitale Composite *C*	53.5	105
Kitale Composite *E*	57.5	113
Kitale II × Ec. 573	62.7	123
Kitale Composite *B* × Kitale Composite *C*	59.8	117
L.S.D. (.05)	5.8	

H611 in yield after 4 cycles of mild selection during the compositing phase. Although no seed of the original entries was retained for comparison, all entries in Kitale Composite *C* were lower yielding than Kitale II. Ec. 573 was the best entry included in this composite and many entries in Kitale Composite *E* were even lower yielding. Although no estimates of variance components are available from these composite varieties, genetic variation in *C* and *E* was expected to be large because of the genetic divergence of the parental varieties and this is verified by current progress. Even more rapid progress is expected from the recurrent selection (S_1 testing *per se*) that is now being initiated.

Empirical comparisons of the various breeding methods were begun in 1964 (Figure 2) to supplement

Table 4. *Estimates of variance components for yield (100 kg/ha) obtained from two replications and four locations in 1964 and 1965.**

Variety	$\bar{x}$	s_g^2	s_{ge}^2	s_e^2	s_{ph}^2
Kitale	46.1	20.4 ± 4.7	12.0 ± 5.9	100.4 ± 7.4	36.0 ± 4.6
Ec. 573	44.2	42.4 ± 7.8	27.3 ± 6.4	91.4 ± 6.7	60.6 ± 7.7
Kitale Composite *A*					
Syn. 1	47.3	21.6 ± 5.8	24.1 ± 8.1	127.8 ± 9.4	43.6 ± 5.6
Syn. 3**	39.6	20.6 ± 3.2	22.5 ± 3.5	67.9 ± 3.6	34.7 ± 3.1

* s_g^2 is the genetic variance (1/4 the additive variance). s_{ge}^2 is the genotype × environmental variance and s_e^2 is the environmental variance. s_{ph}^2, the average phenotypic variance, is equal to $s_g^2 + \frac{s_{ge}^2}{4} + \frac{s_e^2}{8}$.

** Data obtained in 1965 only.

the comparisons possible from prediction formulas. Ec. 573 and Kitale II were chosen as the parental populations since Kitale Composite *B* and *C* had not yet reached HARDY-WEINBERG equilibrium. Since it was not possible to compare all methods in both Kitale II and Ec. 573, Kitale Composite *A* was used for most comparisons except RRS and plant-row selection. Because of the genetic diversity of the parental varieties, genetic variation was expected to be greater in Kitale Composite *A* so that progress from selection should be greater.

Variance components were obtained from the mass selection, plant-row, and reciprocal recurrent selection trials in 1964 and 1965 (Table 4). Comparisons of expected progress for some of the various methods are presented in Table 5. The predictions for plant-row selection are based only on selection among plant-rows and do not include the mass selection within the better plant-rows. Mass and plant-row selection require one year per cycle whereas half-sib selection (recurrent selection for general combining ability with recombination of remnant selfed seed) and RRS require two years per cycle at Kitale. Estimates of phenotypic variances are not yet available for full-sib family selection and for S_1 testing *per se*. These more intensive methods of selection are more effective than mass selection and plant-row selection. If facilities and personnel are limited, however, considerable improvement can be made with mass selection if the refined experimental techniques outlined by GARDNER (1961) are used.

Table 5. *Expected progress for yield per year from different selection methods expressed as per cent of the mean.**

Variety	Selection Method			
	Mass	Plant-row	Half-sib	RRS
Kitale II	–	6	12	–
Ec. 573	–	11	22	–
Kitale II × Ec. 573	–	–	–	7
Kitale Composite *A*				
Syn. 1	–	6	12	–
Syn. 3	8	8	15	–

* Selection intensity is 2% for mass selection and 10% for other methods.

Two cycles of plant-row selection have been completed. Yield trials at 10 locations in 1966 indicated that progress has been made in improving yields (Table 6), though eight to ten years of selection will be required to obtain good evaluation of the relative efficiencies of the various methods. The observed progress in Kitale Composite *A* Syn. 1 is much less than predicted. Even though 3 replications were grown at 10 locations, the L.S.D. indicates that the discrepancy between observed and predicted yields may be due to experimental error. Selection was initiated in the Syn. 1 as well as the Syn. 3 generation to obtain empirical information on the effect of linkage if selection is begun before a population approaches an equilibrium state. HANSON (1959) has suggested a minimum of 4 generations of random mating before intense selection is initiated.

Table 6. *Observed and predicted yields (100 kg/ha) for three varieties of maize and for improved selections from these varieties grown at 10 locations in 1966.*

Variety	Cycle of Selection	Method	Yields	
			Observed	Predicted
Kitale II	C_0		50.9	50.9
	C_1	Plant-row	54.5	53.9
	C_2	Plant-row	53.7	57.0
Ec. 573	C_0		38.7	38.7
	C_1	Plant-row	44.4	43.0
	C_2	Plant-row	47.5	47.2
Kitale Composite *A*				
Syn. 3	C_0		51.2	51.2
	C_1	Mass selection	55.0	55.3
Syn. 1	C_1	Plant-row	53.1	54.3
	C_2	Plant-row	53.2	57.3
L.S.D. (.05)			5.8	

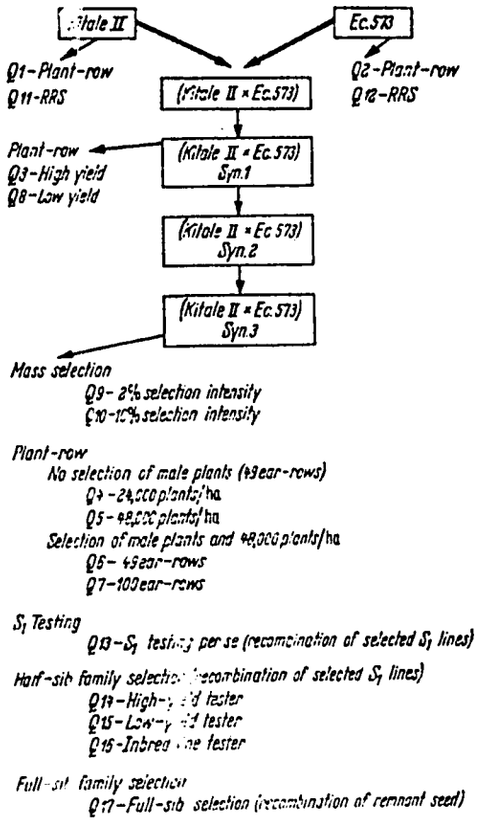

Fig. 2. Recurrent selection methods under evaluation in Kenya.

Applications to Other Crops

This comprehensive breeding system has been extremely effective in improving maize yields in Kenya. Such a flexible system should be easy to modify for other crops and could similarly be used to produce improved varieties. The morphology of maize and the normal outcrossing that occurs make the application of the various breeding methods relatively easy. The application to other cross-pollinated crops should not be difficult, although there are certain limitations, of course. For instance, recurrent selection methods such as mass selection and half-sib selection with recombination of remnant seed would be suitable for sunflowers; whereas full-sib family selection and S_1 testing would be more difficult.

Self-pollinated crops require special techniques to obtain the necessary crossing during recombination. In sorghum this can be accomplished by the use of COES genetic male sterility or cytoplasmic sterility

(DOGGET and EBERHART, in press). In crops where no sterility factors are available, hand crossing may be necessary. The amount of crossing required in this systematic breeding system using heterogenous populations need be no greater than that required in many of the successful current breeding programs in which only paired variety crosses are made.

Zusammenfassung

Es wird über ein umfassendes Züchtungssystem berichtet, das von der Kenya Maize Research Section entwickelt und angewendet wurde. Es umfaßt folgende 4 Hauptphasen:

1. Beurteilung lokaler und fremder Sorten, um das beste Zuchtmaterial verfügbar zu haben.

2. Zusammenstellung des ausgewählten Zuchtmaterials in zwei oder mehr Populationen oder Sorten derart, daß jede Population bezüglich der zu verbessernden Merkmale eine erhebliche genetische Variation aufweist und die Kreuzungen dieser Populationen Heterosiseffekte ergeben.

3. Rekurrente Selektion in jeder Population, um die Häufigkeit brauchbarer Gene zu erhöhen und damit die Populationen und Populationskreuzungen mit jedem Selektionszyklus zu verbessern.

4. Entwicklung einer Handelssorte auf einem der folgenden Wege: a) Kreuzung von 2 Populationen als Sortenhybride, b) Hybriden aus Einzel-, Dreiweg- oder Doppelkreuzungen von Inzuchtlinien, die nach jedem Selektionszyklus aus Elitematerial entwickelt wurden, oder c) eine synthetische Sorte aus einer fortgeschrittenen Generation der Populationskreuzung in Gebieten, wo eine Hybriderzeugung noch nicht möglich ist.

Es werden vorläufige Ergebnisse mitgeteilt, die anzeigen, daß eine züchterische Verbesserung des Maises bei Anwendung dieses Systems möglich ist. Darüber hinaus wird die mögliche Anwendung dieses Systems auf andere Fruchtarten kurz besprochen.

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