IMPROVING ADAPTATION AND YIELD DEPENDABILITY IN MAIZE IN THE DEVELOPING WORLD

R.L. Paliwal and Ernest W. Sprague

IMPROVING ADAPTATION AND YIELD DEPENDABILITY IN MAIZE IN THE DEVELOPING WORLD[1]

R.L. Paliwal* and Ernest W. Sprague**

* Associate Director, CIMMYT Maize Program
** Director, CIMMYT Maize Program

[1] An earlier version of this paper was first presented at the FAO/SIDA Technical Conference on Improved Seed Production, Nairobi, Kenya, June 2-6, 1981.

SUMMARY

This paper concentrates on the problems of maize improvement in the tropics. Studies on the inheritance of characters in maize have contributed significantly to the understanding of both qualitative and quantitative genetics and their application to crop improvement. The maize crop has undergone tremendous genetic improvement, both through the development and improvement of maize populations and open-pollinated varieties, as well as through the utilization of heterosis and the production of various kinds of hybrids. Theoretical studies in quantitative genetics in maize have provided guidelines not only for maize breeding but also for many crops that are outbreeding or lend themselves to outbreeding techniques.

The authors emphasize the necessity for the development and maintenance of broad-based gene pools and populations. They describe CIMMYT's continuous flow system where materials are assembled into gene pools undergoing continuous improvement, the advancement of desirable materials into populations of more specific designation, and the refinement of superior selections to produce high-yielding stable varieties.

International testing plays a major role in this system. Materials are tested as soon as they are able to offer superior germplasm to the countries concerned, and at several subsequent stages of advancement. National cooperators may use the materials at any stage of development, and ultimately make selections for the formation of experimental varieties. To ensure the maintenance of broader adaptation and yield stability, experimental varieties are made also on the selection of superior materials across all sites.

In comparison with the recommended methodology, hybrids require a substantial developmental period before a usable product is obtained. Also, experimental varieties compare favorably with hybrids in yield potential and other desirable attributes after this time period. In addition, whereas hybrid seed needs to be supplied anew at each planting to maintain high yields, seed from varieties can be harvested from the previous crop for several cycles, with appropriate precautions.

The authors go on to describe CIMMYT's research to improve the grain efficiency of tropical maize, to increase drought tolerance, insect and disease resistance, and to improve nutritional quality.

The paper then concludes with a series of important considerations which must be addressed if maize yields in the tropics are to be substantially increased.

Background of maize improvement and production in the tropics

From its center of origin in tropical Latin America, maize has now spread as an economic crop to almost all other tropical areas of the world and to temperate regions as far north and south as 65° latitude and to altitudes as high as 3,000 meters. However, maize has attained the highest levels of production in the temperate areas of the world employing modern agricultural techniques. Although approximately one-half of the world's maize area is planted in the developing countries of Asia, Africa, and Latin America, only one-fourth of the world's maize crop is harvested there. Yields in these areas average less than 1.5 tons per hectare.

Why such a difference in average yield in tropical and temperate regions of the world? One reason is that the maize crop is grown with much higher levels of management in most maize-growing countries in the temperate regions of the world. In contrast, in most of the tropical countries maize is grown as a rainfed crop in the hot season, under varying conditions of moisture, generally subject to periodic and erratic drought and/or excess of water at different stages of the growth cycle, without effective weed and pest control, and usually under low-fertility conditions. In general it is grown as a subsistence crop, with very low levels of management and few inputs.

In those parts of the tropical world where maize is grown as an irrigated crop (not entirely dependent on rain), with adequate inputs and management, its production is quite high. For example yields of five to six tons/ha are not uncommon in the Nile Valley of Egypt and with winter maize in India. Yet, by and large, yield levels in the tropics do not come close to the avergae yields obtained in the temperate areas.

There are reasons other than levels of input and management that contribute to these low yields. Generally speaking the tropical maize plant is not grain efficient. It is too tall, too leafy, and subject to lodging. It has a large tassel, a low grain to stover ratio, and is less responsive to high density and better management as compared with the temperate maize plant.

Also maize improvement work in most of the tropical countries suffered from two serious handicaps. First, research began late and proceeded slowly with very limited facilities and resources. Second, the majority of the national breeding programs were handicapped by the narrow genetic base of the germplasm available to them.

During the 1940s, hybrid maize was developed and became one of the most significant plant breeding advances of this century. Hybrid maize revolutionized maize production and commercial agriculture in the USA and later in Europe. Following this success in the temperate areas, many national programs in the developing world also initiated hybrid development programs, but soon learned that they could not repeat the success story of the USA and Europe under their conditions. The major reasons for this failure were: (a) non-availability of suitable genetic materials for the development of inbred lines; (b) limited facilities and infrastructure, both in terms of physical and financial resources; and, most important of all, (c) lack of effective seed production and distribution systems. Because of these restrictions it was necessary to devise a scheme for the development of suitable materials and seed which would accommodate circumstances of the developing world.

Studies in quantitative genetics indicated that the application of recurrent selection could lead to a significant improvement in maize and in other outcrossing crops. Also, most important for the developing world, this methodology would yield improved varieties that would serve their requirements well. In the face of some skepticism from the successful hybrid breeders of the USA, and despite the lack of firm practical evidence for its success, some population improvement programs were developed to provide varieties with increased productivity potential and better sources for inbred-line development where hybrids could be produced.

Some recent concepts of effective maize breeding

In recent years breeding concepts have been revised considerably as a result of a better understanding of the concepts of population genetics, and various forms of recurrent selection have been used successfully by maize breeders around the world for intra- and inter-population improvement.

Today, many former skeptics have revised their opinions. Sprague and Eberhart (1977) pointed out that information from statistical genetic theory and empirical experiments of many workers suggest many ways in which the effectiveness and efficiency of maize breeding can be improved over the traditional inbreeding and hybridization methods that have evolved over the years.

Lonnquist (1978) stated that the hybrid maize success story in the USA "resulted from the sheer weight of efforts directed towards their development." He added that R.E. Comstock and his colleagues have provided the necessary theoretical knowledge and guidelines for recurrent selection and population improvement which established new trends for maize improvement, and also for many other crops.

Most breeders in the USA still see hybrids as the optimum end product for the U.S. farmer. However they recognize the importance of the achievements and concepts of recurrent selection for population improvement, and they plan to put more effort into such work in the future (Duvick, Hallauer, pers. comms). CIMMYT, with its mandate to assist the national programs in the developing countries, emphasizes open-pollinated varieties as the end product, given the farming situations in most of these countries. Nevertheless, where the requisite infrastructure can be developed to sustain such a program, CIMMYT does assist the national program in venturing into hybrid development.

CIMMYT has designed its program to accommodate these requirements, and this program can be adapted for use on any outbreeding crop with very few modifications.

CIMMYT's multistage and integrated maize improvement program

Various aspects of CIMMYT's maize breeding program have been described in detail by Johnson (1974), Vasal et al. (1978), and Ortega et al. (1980). This program is designed to a) provide an overall strategy that can effectively serve different maize-growing areas around the world having diverse levels of capability; b) serve as a mechanism for continuous development and improvement of maize germplasm to meet current and future needs; c) provide a smooth and efficient delivery system to and from the national programs; and d) meet the needs for exploratory and innovative maize research. Its emphasis is on the development and improvement of broad-based gene pools and populations leading to the development of superior varieties in both normal and quality protein materials. It is a multistage process with a continuous and systematic flow of germplasm from CIMMYT's germplasm assembly line to the farmer's field, with national programs participating as effective cooperators.

CIMMYT believes that the development and improvement of broad-based gene pools should be the backbone of every aggressive maize breeding program. This approach is the best insurance against genetic erosion and vulnerability due to a narrow gene base (Sprague and Finlay, 1976) and also provides a source of superior germplasm for current and future breeding programs.

Each pool is a reservoir of the necessary genetic variability to serve a range of known conditions and is a source of germplasm for the continuous flow improvement process which selects and refines populations for more and more specific conditions as the program advances. The system of pool management at CIMMYT is handled in what is called the Back-Up Unit, and the subsequent refinement of populations is handled in the Advanced Unit.

There are three main stages in the system:

1) Development and improvement of broad-based gene pools for different specified areas of the world.

2) Continuous improvement and refinement of populations with upgraded material from the corresponding pool.

3) Selection of superior experimental varieties from populations.

International testing plays a major role in the selection of improved materials. The testing begins as soon as the populations are considered to be sufficiently advanced to offer something to the national programs. The national programs may use these materials as they see fit; some promising materials that may have something to offer the farmer could be put to use immediately. Also national programs may further select and refine the materials to suit their conditions, or incorporate the materials at various stages into their breeding programs. Some national programs may utilize the materials in a hybrid program. Although the emphasis is on intrapopulation improvement with open-pollinated varieties as the end product, information is collected and made available to national programs on the heterotic response among various populations for interpopulation improvement and for the development of hybrids.

The salient features and significant achievements of these procedures, particularly with reference to improvement of adaptation and yield dependability, efficient input use, and meeting the needs of farmers and consumers are discussed in the following sections.

Development of broad-based gene pools as germplasm resources

Most maize breeding programs around the world are working with rather narrow genetic bases, despite the fact that they may be handling a large number of materials. An important activity of CIMMYT's maize program is to develop broad-based gene pools as functional germplasm resources. Genetic diversity and variability are basic requirements for any successful population improvement program.

A gene pool is a mixture of diverse germplasm, undergoing continuous recombination, from which materials can be extracted and to which materials can be added. CIMMYT currently has a total of 27 gene pools to accomodate preference in grain type and color, maturity requirement, and environmental adaptability. There are 12 gene pools for the tropical-lowland zone, eight for the subtropical-temperate zone and seven for tropical-highland areas.

A modified half-sib method of selection is used for the recombination and improvement of gene pools. The size of a pool is maintained at approximately 500 families. This number is manageable and maintains a high level of genetic variability. The 500 families making up a gene pool are planted in a ratio of 2 female: 1 male rows. The pollinator is a balanced seed mixture of superior families. For traits expressed before flowering, selection pressure is exercised by also detasseling undersirable plants in the pollinator rows.

Each pool is grown at more than one site. Superior families are identified at each location by a team of scientists from various disciplines. Yield potential, height, maturity, lodging, disease and insect reaction, and uniformity are taken into account at appropriate stages of plant development. Best plants are identified at each location only in those families which have performed well at all locations. At harvest, the best ears are chosen from the selected plants for each pool at each site.

In addition, ears from families found greatly superior at only one site are also retained to provide potential superior recombinants for the future. They are planted as female rows only and their seed is not included in the bulk to be used as pollinator. This selection on the basis of across-site performance widens the adaptability of the pool, while still retaining superior performers at specific sites.

Introductions and the additions from the germplasm bank are planted only as female rows and therefore are always detasseled. This avoids the possibility of unproven materials contaminating the pool and provides the opportunity of comparison of the introductions with the pool, while they are being crossed to it. Selected ears from superior introductions are again planted as female rows in the next cycle to obtain an indication of their potential and possible introduction into the pool. Superior and suitable introductions thus identified are merged with the pool.

Development of new sources of genetic variability

As mentioned earlier, most of the breeding programs in Europe and in the USA, where the highest yields of maize are obtained, are handling materials with a relatively narrow genetic base. In recent years maize researchers in these countries have become concerned with the dangers of genetic erosion. CIMMYT believes that tropical maize has economically desirable traits of potential value in temperate germplasm, and that tropical maize could itself benefit from the introduction of certain characters from temperate maize (Sprague, 1977). In order to facilitate the introduction of exotic germplasm into temperate materials, which in turn will serve to transfer superior characters from the temperate germplasm into the tropical lowland and highland materials, CIMMYT has developed four gene pools of wide genetic diversity. The basic principles in putting together such broad-based gene pools, their recombination, and later multilocational evaluation and selection has been described by Sprague (1977).

The first of these pools was initiated in 1976 as a joint effort between the University of Hohenheim, Germany, and CIMMYT. Based on our experiences in the development of this pool, CIMMYT has since assembled three other broad-based gene pools:

1. NTR, for the northern temperate climatic ranges.
2. ITR, for the intermediate belts of temperate regions.
3. STR, for the southern temperate ranges.

(Similar ranges in the southern hemisphere correspond to the northern hemisphere, but in reverse order.)

The CIMMYT-German gene pool consists mainly of a mixture of lowland and highland tropical maize with very little temperate material. The NTR gene pool is based on materials from the U.S. Corn Belt, the STR pool is based on U.S. Corn Belt plus tropical lowland and highland materials, and the ITR pool involves primarily maize materials from Europe. After these pools have been thoroughly recombined, they will be subjected to multilocational screening, evaluation, and selection, followed by recombination of selected families at CIMMYT.

Improvement of maize populations and development of experimental varieties

Farmers' conditions usually demand materials of specific adaptability, maturity, and seed type. To serve this demand, the Advanced Unit is currently handling 27 maize populations (23 normal and four quality protein maize populations carrying the opaque-2 gene). At this stage, international testing in the different environments becomes necessary. One full-sib cycle of selection and international testing of progenies from each population can be completed every year. However, the retrieval of trial data from cooperating countries located both in the northern and southern hemisphere makes it difficult to complete the full cycle in one year, and therefore a two-year cycle is used. The following steps are involved (see Fig. 1).

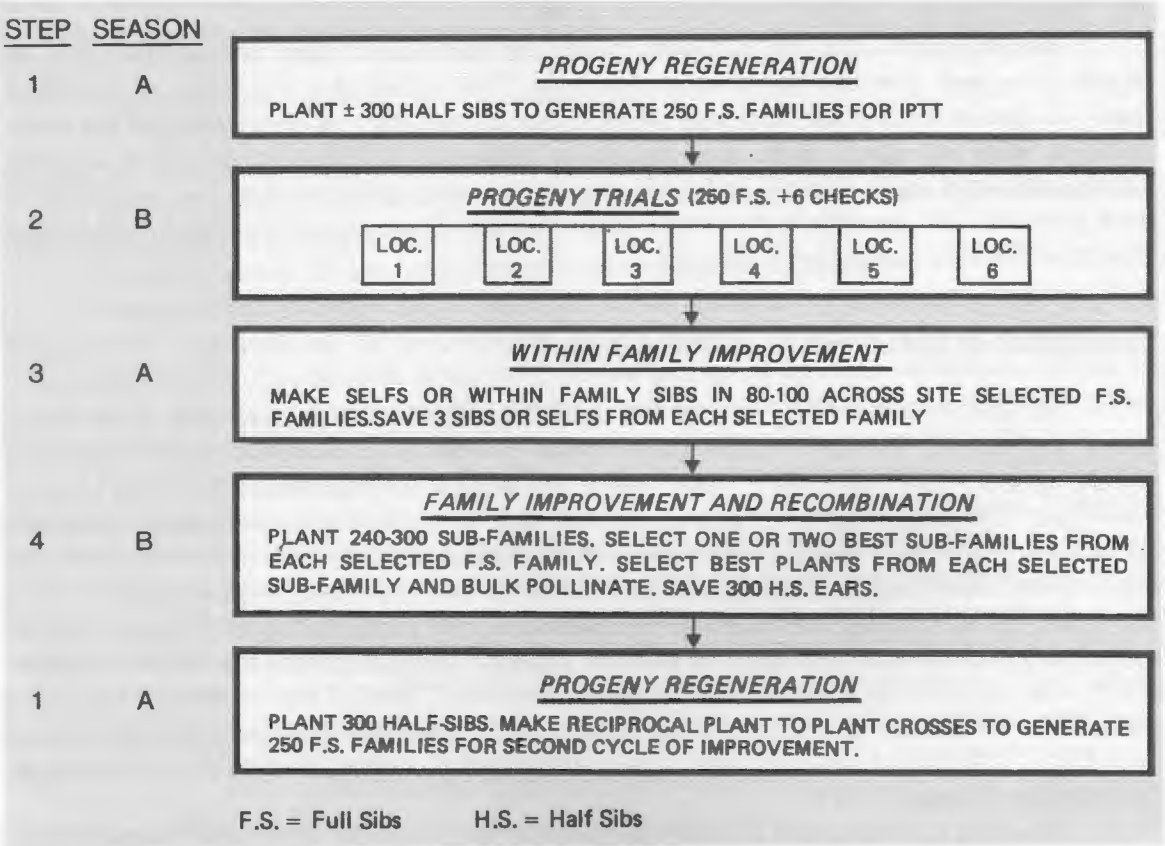


Fig. 1. Population improvement scheme breeding sequence

1) **Full-sib progeny regeneration**: To maintain the requisite number of families and provide sufficient full-sibs for desired selection pressure at this stage of advancement, each population is maintained with about 100 families, and 250 full-sibs are developed each cycle through reciprocal plant-to-plant crosses among the families. Selection is exercised for maturity, plant and ear height, disease and insect resistance, and good agronomic characters. Reciprocally-crossed ears are bulked to provide sufficient seed for six tests, enough remnant seed for generating the next selection cycle, and for the development of experimental varieties using selected families.

2) **International progeny testing trials (IPTTs)**: 250 full-sibs plus six checks are tested the next season, at six different sites in three to six countries, using a 16 x 16 simple lattice design with two replications. Based on across-site analysis, 80-100 families are selected for the generation of the next cycle's population. The superior ten families from each site and ten best across-site families are identified for development of experimental varieties.

3) **Family improvement**: Within-family selection is made for the deficient characteristics. This selection is restricted to the families selected on the basis of data retrieved from international trials (IPTTs). Selfs or sibs are made within each selected family.

Within-family sibs are usually made for the improvement of characteristics that can be observed before flowering, such as earliness, and plant and ear height. In opaque-2 populations, where the aim is the selection of better modifier genes for endosperm hardness, reciprocal plant-to-plant crosses are made. For other characteristics, where the plant expression can best be judged at harvest time, either selfs or reciprocal plant-to-plant crosses are made so that both parents can be identified and observed at that time. At harvest, an average of three sibs or selfs are saved from each family.

4) **Half-sib recombination of selected families**: The sibs or selfs (sub-families) saved from each family are thoroughly recombined the following season. Selection for the traits concerned are again made both among and within sub-families and pollinated in a hand-pollinated half-sib fashion. An average of three half-sibs are selected from the progenies of each original parental full-sib family that was selected based on its across-location performance.

5) **Full-sib progeny regeneration for next improvement cycle**: The selected half-sib ears are planted on an ear-to-row basis. A record is kept of all half-sibs originating from each parental full-sib family. Reciprocal plant-to-plant crosses are made among half-sib families originating from different parental full-sib families. At harvest, 250 full-sib pairs are saved to continue the next cycle of selection.

Development of experimental varieties

A selection intensity of four percent is used in the selection of families for the development of experimental varieties. Experimental varieties are developed both on the basis of site-specific and on across-site progeny test data. Since the best fraction of each population is used to form the experimental variety, it is expected that these varieties will show considerably higher performance as compared to the population mean. In addition to those characters that establish a variety, uniformity for maturity and plant and ear height are important considerations in the selection of the ten best families so that the resultant variety is uniform in appearance.

Each experimental variety goes into a second-order seed increase to build up a sufficient quantity of seed. Thus, if a variety proves to be promising in the Experimental Variety Trial (EVT), it can be used immediately in the second series, called Elite Experimental Variety Trial (ELVT).

Variety names are derived from the names of stations where the progeny test was conducted, and, therefore, where in fact that variety was made. For pedigree purposes this name is followed by two digits indicating the year in which the selection was made, then two digits showing the population number from which the variety is derived, e.g., Tocumen 7928, selected in 1979 from population 28.

Progress from recurrent selection in CIMMYT's maize populations

The progress in recurrent selection made over two to three cycles in 13 populations is given in Table 1. Base populations and improved cycles (C_2 or C_3) of these populations were tested in a split-plot design (populations as main plots and cycles as sub-plots) in replicated trials (four replications) at three sites in Mexico. The results of the trial are summarized in Table 1. All 13 populations showed improved yield, earlier maturity, and reduced plant height. The gains per cycle for yield ranged from 0.75 to 9.8 percent, averaging 3.44 percent per cycle over all populations.

Some populations, for example, Mezcla Tropical Blanca and ETO Blanco, showed relatively lower gains (1.44 and 0.75 percent, respectively). This would tend to indicate that the additive genetic variance for yield, which is the component of variance exploited in population improvement, is rather low. It may be wise to introgress into these populations superior genetic fractions from the corresponding Back-Up gene pools. This will widen the genetic variability of these populations, and recurrent selection for improvement could be continued with success.

Nevertheless, these two populations *per se* have a very high yield potential. This factor has been exploited to develop high yielding and phenotypically acceptable varieties. One of the best varieties which has given very good performance in several countries around the world, La Maquina 7422, came out of Mezcla Tropical Blanca.

Populations La Posta and Cogollero showed relatively high gains per cycle, i.e., 5.2 and 9.8 percent, respectively. La Posta has produced superior varieties which are comparing favorably with national check hybrids in several areas of Central America and Africa. While La Posta was handled as a closed population, Cogollero, after the first cycle of improvement, was merged with the superior genetic fraction of another population, IDRN; this may explain the high gain seen in this population.

A significant fact that has emerged by implementing this breeding methodology is that across-location varieties, developed from multilocation IPTT data, are showing a progressively greater degree of wide adaptation and increasing yields at several locations. Across-location data indicate that across-site varieties are now giving stable and top performances at several locations. Examples of such varieties are: Across 7822, Across 7728, Across 7736 and Across 7740.

Another salient feature emerging from the international trial data is that certain test locations appear to have a combination of environmental factors such that site-specific progeny selections for the development of varieties have resulted in varieties that give top performance at several other geographic sites. Examples of such locations are: La Maquina in Guatemala, Tocumen in Panama, San Andres in El Salvador, Poza Rica in Mexico, and Ferkessedougou in the Ivory Coast.

Table 1. Gains following 2 to 3 cycles of selection in 13 populations

No.	Population Name	Cycles of Improvement	Total percent gain	o/o gain per cycle/year
21	Tuxpeño - 1	2	4.4	2.20
22	Mezcla Tropical Blanco	3	4.3	1.44
23	Blanco Cristalino - 1	3	6.6*	2.20
24	Ant. x Ver. - 181	3	10.6**	3.50
25	(Mix. Col. Gpo. 1) x Eto	2	4.8	2.40
26	Mezcla Amarilla	2	6.2	3.10
27	Amarillo Cristalino	3	13.6**	4.50
28	Amarillo Dentado	2	5.9	2.90
29	Tuxpeño Caribe	2	5.4	2.70
32	ETO Blanco	2	1.5	0.75
35	Ant. x Rep. Dom.	2	8.1*	4.05
36	Cogollero	2	19.7**	9.80
43	La Posta	3	15.7**	5.20
X			7.9**	3.44

* and ** significant at the 0.50 and 0.01 level of probability, respectively

One of the test sites in these comparison trials was Ciudad Obregon, Mexico, which represents a heat and moisture stress environment. The improved cycles showed a much greater yield advantage over the parent populations at Ciudad Obregon as compared to two other sites which had more favorable environmental conditions and were not subject to either of these stresses.

The above results demonstrate the effectiveness of the full-sib population improvement system in conjunction with multilocation testing to improve yield and wider adaptability of the populations and of the experimental varieties.

Sprague and Eberhart (1977) have listed average yield gains per cycle in intra- and inter-population improvement by various authors using different recurrent selection schemes. The average gain per cycle for each scheme (average of all populations reported) is summarized in Table 2.

The average selection gain of 3.44 percent per cycle (with one cycle per year) observed in CIMMYT populations, along with improvement in other agronomic characters such as earlier maturity and reduced plant height, compares favorably with the recurrent selection results achieved by other workers.

Table 2. Average gains obtained with different selection schemes

Scheme	Number of populations reported	Range of gain/per cycle, o/o	Average gain/per cycle, o/o
Intrapopulation Improvement			
Mass Selection	6	1.4 – 11.1	3.40 (1.9 if one Tropical population showing excessively high gain of 11.1 o/o per cycle is excluded)
Ear to Row	6	2.2 – 5.3	3.78
Full-sib	5	2.5 – 4.0	3.12
S_1 Selections	6	1.1 – 6.9	4.65
S_2 Selections	2	1.9 – 2.2	2.05
Test Cross	4	0.7 – 7.3	2.85
Interpopulation Improvement			
Reciprocal	9	0.4 – 7.4	2.90
Test Cross (variety tester)	8	1.4 – 3.8	2.65
Test Cross (inbred tester)	7	1.8 – 7.4	4.48

Gains in yield of varieties over the parent populations

In the CIMMYT program the selection intensity for families to regenerate the next cycle of the population is 30 to 40 percent, while the selection intensity for families to generate experimental varieties is four percent. A comparison of eight open-pollinated varieties with their parent populations of the same cycle, tested at 12 to 19 locations, is presented in Table 3. These were the first cycle of experimental varieties produced following the implementation of the full-sib family selection and international testing system. The

Table 3. Yield gains in open-pollinated varieties over the original populations

Variety		Population	Yield of Variety as Percent of Population Mean Across Locations
Gemiza	7421	Tuxpeño 1	112
Poza Rica	7422	Mezcla Tropical Blanco	107
Tocumen	7428	Amarillo Dentado	117
Rampur	7433	Amarillo Subtropical	111
Yousafwala	7435	IDRN	115
Tlaltizapan	7443	La Posta	119
Tlaltizapan	7444	AED x Tuxpeño	120
Pirsabak	7448	Compuesto de Hungary	108

mean gains across locations ranged from 107 to 120 percent. Similar results are observed in quality protein materials. The superiority in yield and in other agronomic characters of experimental varieties extracted following each cycle of intrapopulation improvement is evident.

Sprague and Eberhart (1977) suggest that the rate of improvement of hybrids from the improved populations will be proportional to the improvement of the population cross between two breeding populations. They further indicate that with a four percent selection intensity, the superiority of double-cross hybrids expressed as a percentage of the population cross mean ranges from 9.4 to 12.4 percent, while the superiority of single-crosses ranges from 15 to 20.4 percent. The yield superiority will increase with the increase of the selection intensity.

Gardner (1978) suggested that if population improvement can be achieved without a significant reduction in genetic variability, the best double-cross and single-cross hybrids from a series of random lines derived from the improved population will exceed the population mean by at least 20 to 30 percent.

Sprague and Eberhart (1977) have shown an expected distribution of best hybrids that can be obtained from an original and improved population. With CIMMYT's methodology the best experimental varieties are extracted following each cycle of improvement. This is represented graphically in Figure 2.

Figure 3 shows the time lag, in seasons, in the development of varieties and hybrids, and their expected performance level based on the selection pressures exerted in CIMMYT's program for open-pollinated materials, and as postulated by Sprague and Eberhart (1977) and by Gardner (1978) for hybrids. A 40 percent selection intensity in an open-pollinated population should give five percent progress each cycle. In CIMMYT's program a variety could be 15 percent superior to the parent population. On the other hand a hybrid could show an approximate 25 percent superiority. However, hybrids require a substantial time lag (11 cycles) for their development. It can be seen very clearly that CIMMYT's program can provide usable materials of superior performance at each cycle of development. Both populations and varieties improve proportionally with each selection, and after the same number of cycles there is very little difference in the performance of hybrids versus varieties.

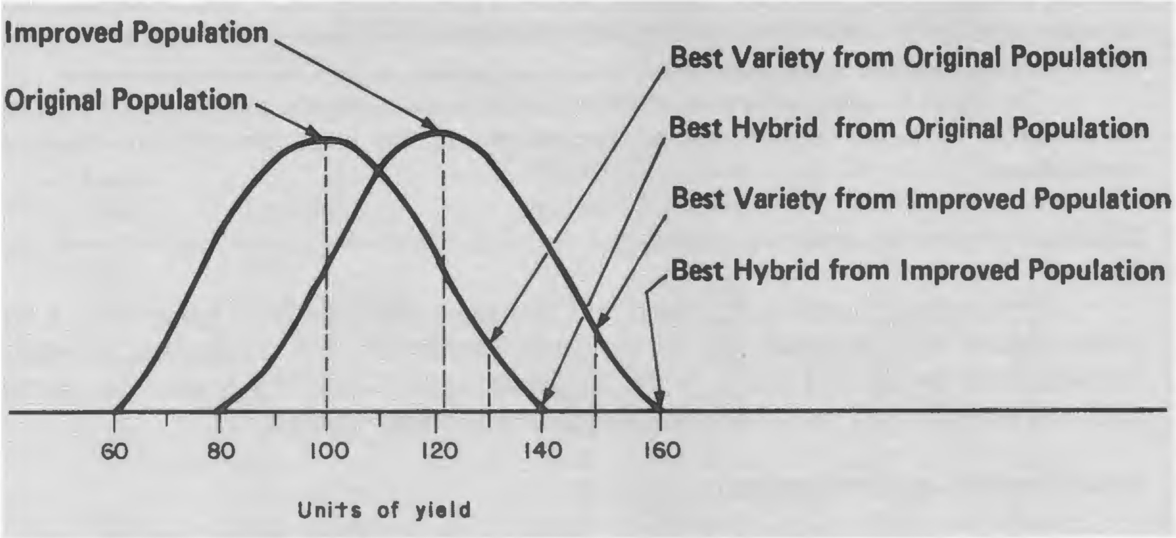


Fig. 2. Expected distribution of yield for single cross hybrids and varieties from original and improved populations (adapted from Sprague and Eberhart, 1977).

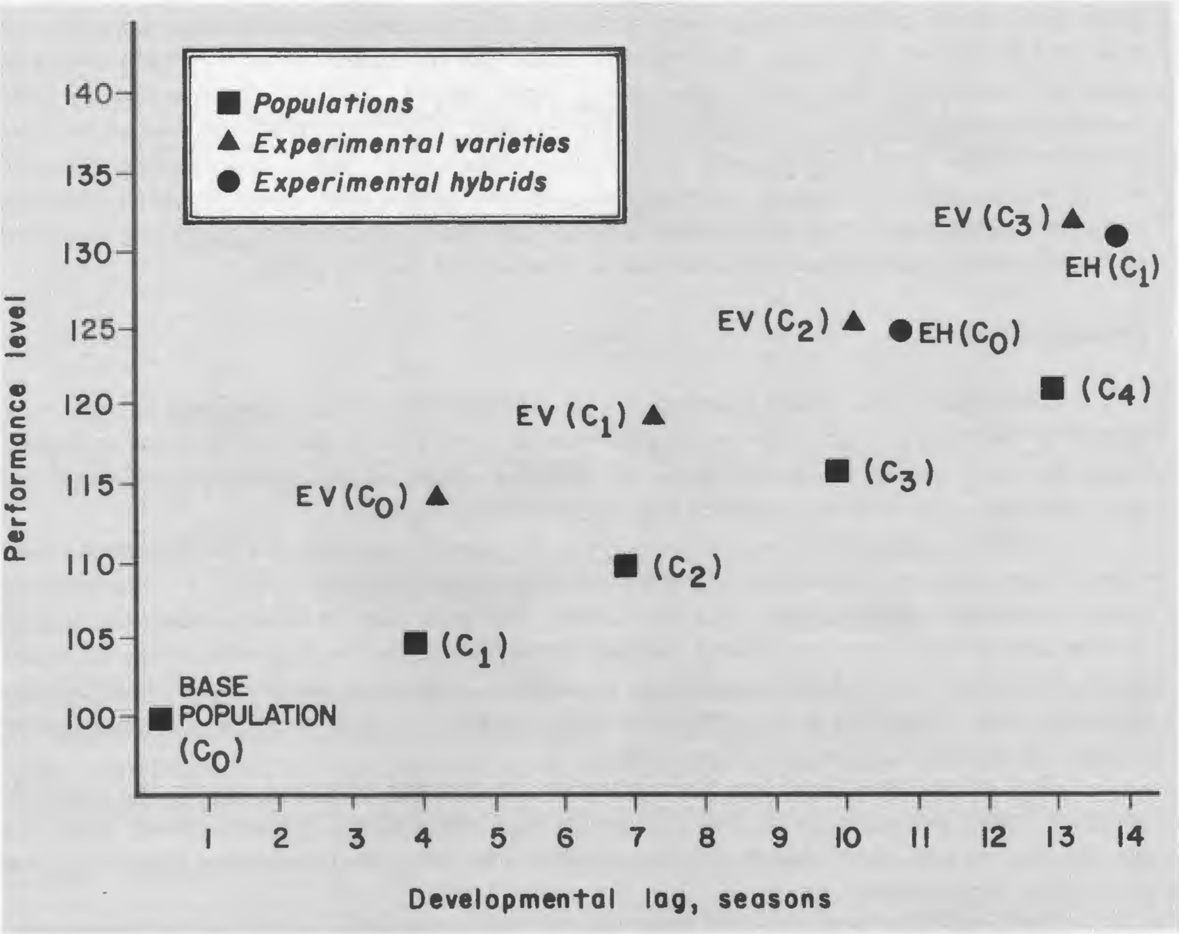


Fig. 3. Developmental time lag for the production of varieties and hybrids

In fact, provided that adequate selection has been practiced in each cycle, varieties could be even superior in performance to hybrids. Performance of some such varieties in multilocation trials is presented in Table 4.

For most national programs in the developing countries the extraction of superior experimental varieties from improved populations is the most cost-efficient breeding methodology.

Selection for environmental adaptability

As indicated earlier in this paper, the tropical maize plant is, in many ways, a less efficient plant in comparison with its temperate counterpart, and is subjected to various environmental stresses not found in the temperate world. CIMMYT's program focuses on the improvement of the most important deficiencies of these materials.

Improvement in grain efficiency

It is appropriate here to describe the results of a long-term recurrent selection program for the reduction of plant height in a tropical maize population, Tuxpeño 1. Major emphasis was on plant height, and only routine selection was made for other characteristics normal to a plant improvement program. The data are presented in Table 4. There was a large and nearly linear reduction in plant height (resulting from reduction in the total number of nodes as well as mean internode length below the ear), and a linear increase in grain yield (when different cycles were grown at their optimum density) at an approximate rate of 2.9 percent per cycle. The harvest index also increased linearly. Fifteen cycles of selection resulted in one meter reduction in plant height, 2.68 tons/ha increase in yield (at optimum plant density), seven day reduction in days to 50 percent silking, and an increase in harvest index from 0.30 to 0.46. This study demonstrates that it is not only possible to reduce plant height of tropical maize, which reduces lodging and makes it more responsive to better management, but that yield efficiency can also be improved through improvement of harvest index (Johnson and Fischer, 1979, Fischer and Palmer, 1980).

Drought tolerance

Throughout the maize-growing regions of the tropics, the maize crop is often subjected to periodic drought due to irregular rainfall distribution during the growing season. Thus the crop suffers moisture stress at different stages of the growing cycle, and this becomes even more critical in soils of low water-holding capacity.

CIMMYT scientists have been studying the genetic variation for performance under water-stress situations and exploring the reliability of easy selection criteria for the development of drought-tolerant types on a field scale. Although there was little measured change in the relative performance among varietal genotypes tested over a wide range of water stress conditions in the base population, Tuxpeño 1, individual families from that population did vary. Therefore a recurrent selection program for improved performance under drought stress was initiated in this population.

The parameters used for the evaluation of drought tolerance under the multiple selection index are (a) relative leaf elongation rate, (b) interval between pollen shedding and silking, (c) leaf tissue death, (d) grain yield under stress and non-stress situations, and (e) canopy temperature.

The results to date show (i) there is a genotype x moisture environment interaction; (ii) that selection under non-limiting moisture conditions does not adversely affect the performance of the material under stress conditions, and that multilocation testing and the selection of families on the basis of across-site performance may enhance performance

Table 4. PCCMCA uniform yield maize trial 1980[1]

Entry No.	Variety	Yield kg/ha	Percent over check	Days to flower	Plant height cm
30	B-666	5703	111	58	269
14	Poza Rica 7843*	5544	108	57	250
17	Poza Rica 7822*	5381	105	56	231
5	ICTA T-101	5364	104	56	236
32	7904	5350	104	57	238
16	La Maquina 7843*	5344	104	58	252
31	7901	5322	104	58	252
1	ICTA HB-33	5309	103	56	229
20	CENTA H-9	5230	102	56	254
36	CENTA H-5	5136	100	57	254
4	La Maquina*	4652	90	58	242

[1] Programa Cooperativo Centroamericano para el Mejoramiento de Cultivos Alimenticios

* Open-pollinated variety

Table 5. Comparison of cycles of selection in Tuxpeño 1

Cycle of Selection	Plant Height (cm)	Grain Yield (t/ha)*	Total dry matter (t/ha)	Harvest Index
0	273	4.05	14.94	0.30
6	211	5.54	14.75	0.38
9	203	5.67	15.32	0.39
12	196	6.18	15.37	0.41
15	173	6.73	15.12	0.46
LSD P.05	10	0.41	1.84	0.05

* Grown at "optimal" densities

under intermediate levels of moisture stress; (iii) that a multiple selection index can be used to identify genotypes (families) that give better than average performance under moisture-stress conditions without detriment to their performance under more favorable conditions or no-stress situations.

Disease resistance

The maize crop is affected by numerous diseases; this is one of the important causes of yield instability, particularly in the hot and humid tropics. Development of reliable polygenic resistance (field resistance/tolerance) against these pests is desired because of its contribution to yield stability. In CIMMYT's recurrent selection program of population improvement, selection pressure is exercised continuously for resistance to ear and stalk rots (using artificial inoculation techniques), and for leaf blights and rusts (using reliable field inoculations). Results of international trials show that the level of resistance to these diseases has improved considerably in several pools and populations.

An example of international cooperation in the development of disease resistance is provided by CIMMYT's collaborative research for downy mildew and corn stunt resistance. In 1974, a collaborative research project was initiated with national programs for screening germplasm in endemic areas. Thailand and the Philippines collaborated for downy mildew screening, and El Salvador and Nicaragua collaborated for corn stunt resistance. The breeding procedure involved the screening of approximately 500 families from each population for disease reaction, the selfing of resistant plants in the respective country, and the recombination among those selections in Mexico, together with selection for desired agronomic characters. This procedure has been repeated for four cycles in three broad-based populations and progress has been made in building up resistance to both downy mildew and corn stunt. These populations are now being used for the development of open-pollinated varieties for downy mildew and stunt affected areas, and by programs interested in hybrid development which are using these populations as sources for resistant inbred lines.

Insect resistance

Insect damage is another important yield-limiting factor. Effective and judicious use of insecticides would appear to be an easy solution to the problem, but our experience in the tropics has shown that such is not the case. Breeding for resistance and/or tolerance to insects has been a continuing concern of maize breeders. This subject has been recently reviewed by Ortega et al. (1980), who described in detail the techniques employed for mass rearing, artificial infestation, and evaluating plant reaction to insect damage.

In 1974 CIMMYT set up an insect-rearing laboratory to produce enough insect larvae to artificially infest and screen maize pools and populations for insect reaction. This laboratory produces millions of larvae of fall armyworm, earworm, sugarcane borer, and southwestern corn borer. Techniques have been perfected for the application of these larvae to thousands of maize progenies through a small dispenser (called a Bazooka) with which one can apply a specified number of larvae per plant with a variation of ± 10-15 percent. This simple technique now has been adopted by maize scientists all over the world engaged in the development of resistance to insects.

Following the development of these techniques considerable progress has been made in improving resistance to fall armyworm in two pools and in two Advanced Unit populations. We hope to make similar progress in sugarcane borer, southwestern corn borer, and earworm resistance.

Improvement of nutrition quality

Improvement of maize for industrial and nutritional quality has received considerable attention from maize breeders over the years. CIMMYT has been concerned with the improvement of nutritional quality of maize through the improvement of protein quality.

Following the discoveries of the biochemical effects of the opaque-2 gene on the maize endosperm and of the nutritional advantages of this maize with modified protein (enhanced levels of lysine and tryptophan), maize breeders around the world initiated breeding programs to upgrade the protein quality of maize. Hybrids and varieties carrying the opaque-2 gene for improved protein quality were developed. These, however, did not find acceptance with the farmers nor the consumers due to several defects associated with the opaque-2 gene. These were soft chalky kernels with a dull appearance, greater vulnerability to diseases (e.g., ear rot) and to pests, slower drying and therefore higher moisture content at harvest, and, most important, reduced grain yield.

To remedy these problems CIMMYT scientists exploited the genetic modifiers to develop hard endosperm opaque-2 materials which appear more like normal maize but still retain superior protein quality. These efforts to accumulate genetic modifiers have demonstrated conclusively that most of the problems confronting opaque-2 maize can be overcome through careful and systematic selection for hard endosperm opaque-2 kernels.

As already mentioned, CIMMYT's maize improvement program stresses the importance of the development and improvement of maize populations and open-pollinated varieties both in normal and quality protein maize. Thus, breeding approaches and selection schemes for intrapopulation improvement are essentially the same, both for quality protein and for normal maize. Because of its peculiar problems, however, for the introduction and maintenance of the opaque-2 gene, and for the accumulation of its modifiers, a backcrossing and recurrent selection scheme (Figure 4) is being used.

The progress made in the development and improvement of normal-looking hard endosperm maize is illustrated in Figure 5. We now have maize materials which are equal to or superior to normal check materials under cultivation in some countries of Central and South America, Africa, and Asia. The problems of reduced yield, vulnerability to ear rot and stored-grain pests, and the dull and chalky appearance have largely been overcome. CIMMYT scientists are convinced that it is possible to combine the beneficial effects of the opaque-2 gene with superior yield and to develop quality protein maize which can be commercially exploited.

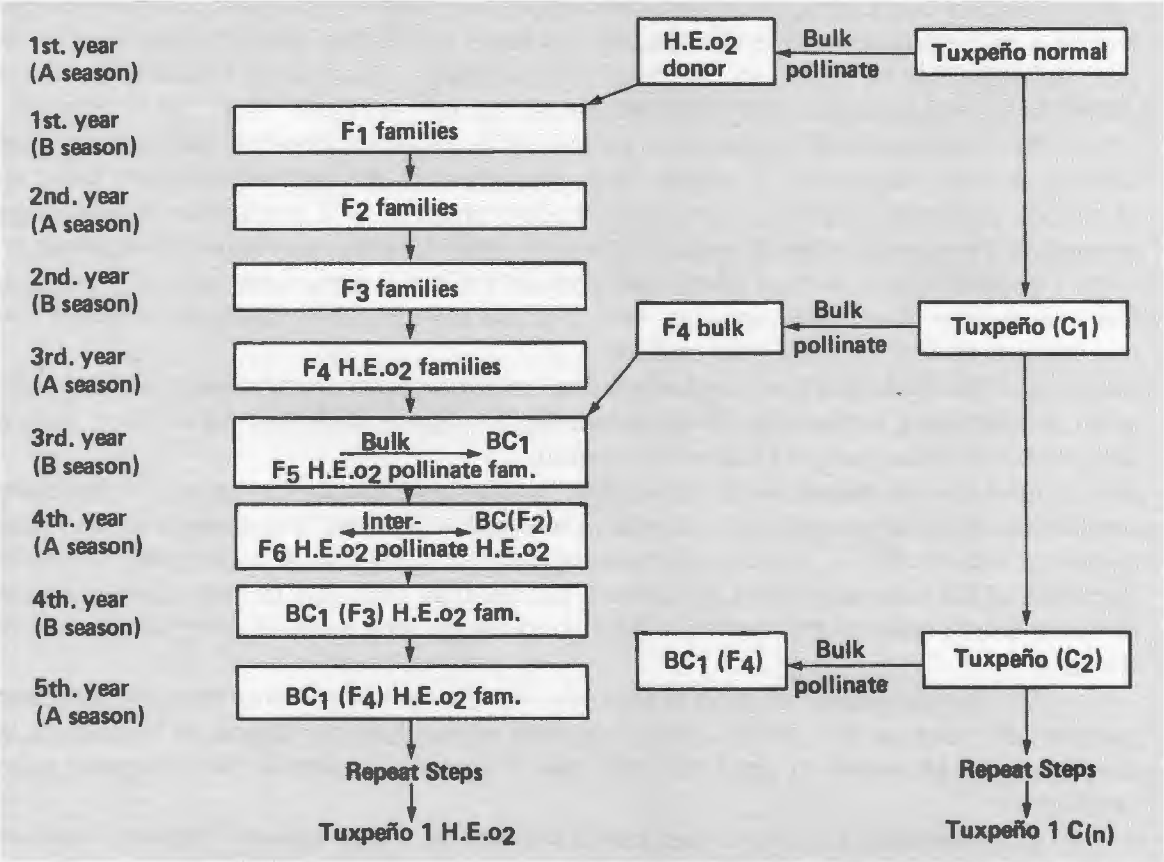


Fig. 4. Backcrossing-cum-recurrent selection scheme for obtaining quality protein maize versions of normal populations undergoing improvement

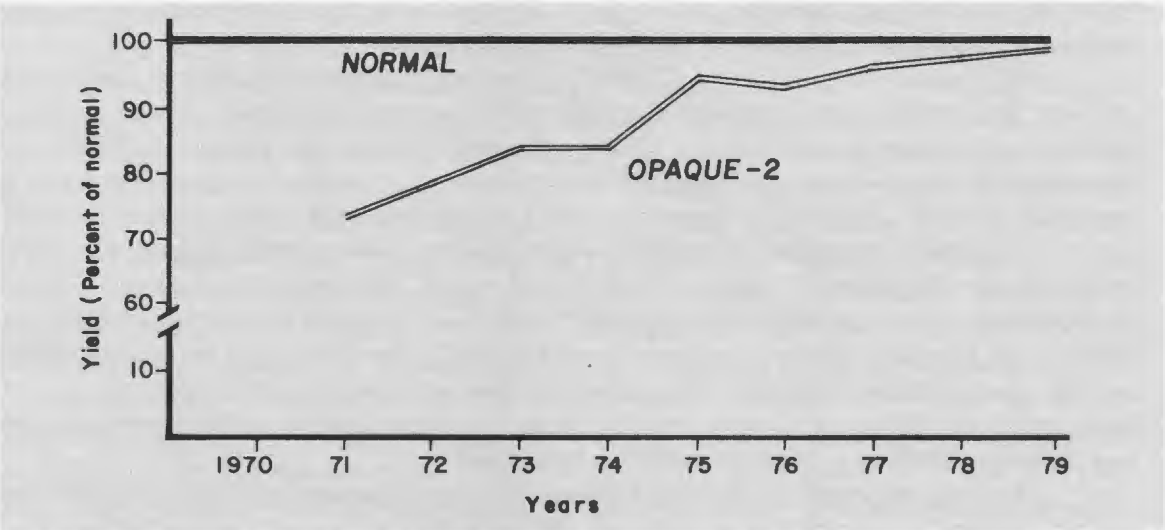


Fig. 5. Grain yield of superior opaque-2 maize expressed as a percentage of normal maize check in different years across all test locations

Important considerations for increasing maize yields in the tropics

We would like to conclude by emphasizing several points which we consider to be vital for maize improvement in most developing countries:

a) There are numerous improvement schemes already available to plant breeders. Every breeding methodology has some advantages and some drawbacks. Too often breeders choose a technique reported to be the best by some authorities, without realizing that no one technique can be suited to all situations and needs. Therefore a breeding technique should be viewed as a means and not as an end.

b) Not only is it necessary to choose an appropriate breeding methodology, but equally or more important is proper field execution of the technique. Again there are numerous examples where a conventional hybrid program or a population improvement program did not yield expected gains because of limited facilities and/or poor execution.

c) For many parts of the tropical world the maize germplasm currently available has a reasonably good yield potential, well over the average yields currently obtained. The overriding need is to increase yield stability.

d) The farming situations under which maize is grown must be taken into consideration in planning a maize research and production program. The need for on-farm surveys and experimentation cannot be over-emphasized.

e) Lack of proper seed production programs is a critical factor limiting maize production in most developing countries. The success of several private hybrid seed companies in the developed world is attributable mainly to two factors: (a) they developed materials which were acceptable to farmers, and (b) they were able to make timely delivery of good quality seed to the farmers. There is no reason why national programs cannot do the same.

f) The production of good quality seed has the same importance for open-pollinated varieties of maize as for hybrids. Seed industries do not have to depend on hybrids to be successful. Development of good national seed programs is essential for increasing maize production.

g) Technology for hybrid maize seed production is well known. There is, however, only scanty information on the maintenance and production of seeds of open-pollinated varieties. It is a matter of satisfaction that added attention is currently being given to the problems of seed production, marketing, and distribution of open-pollinated varieties.

LITERATURE CITED

Fischer, K.S., and Palmer, A.F.E. 1980. "Yield Efficiency in Tropical Maize." Paper presented at Symposium: "Potential Productivity of Field Crops Under Different Environments," IRRI.

Gardner, C.O. 1978. "Population Improvement in Maize." In *Maize Breeding and Genetics* (Ed. D.B. Walden), John Wiley and Sons Inc., pp. 207-228.

Johnson, E.C. 1974. "Maize Improvement." In Proceedings of World-Wide Maize Improvement in the 70s and the Role for CIMMYT. Mexico. pp. 3.1 - 3.37.

Johnson, E.C., and Fischer, K.S. 1979. "Ideas para Mejorar la Eficiencia de Variedades de Maíz." Twenty-fifth PCCMCA meeting, Tegucigalpa, Honduras.

Lonnquist, J.H. 1978. Introductory Remarks to the Session on Corn Breeding. In *Maize Breeding and Genetics* (Ed. D.B. Walden), John Wiley and Sons Inc., pp. 187-189.

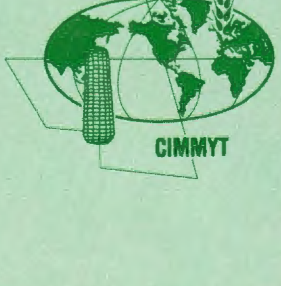
Ortega, A., Vasal, S.K., Mihm, J., and Hershey, C. 1980. "Breeding for Insect Resistance in Maize." In *Breeding Plants Resistant to Insects* (Ed. F.G. Maxwell and P.R. Jennings), John Wiley and Sons Inc., pp. 371-419.

Sprague, E.W. 1977. Development of New Sources of Genetic Variability for Europe. In Proceedings of the IXth Meeting of Eucarpia; Maize and Sorghum Section. Krasnodar, 1977, pp. 112-128.

Sprague, E.W., and Finlay, K.W. 1976. "Current Status of Plant Resources and Utilization." Paper presented at "The World Food Conference of 1976." CIMMYT reprint No. 19.

Sprague, G.F., and Eberhart, S.A. 1977. "Corn Breeding," in *Corn and Corn Improvement* (Ed. G.F. Sprague), American Society of Agronomy, Inc., pp. 305-362.

Vasal, S.K., Ortega, A., and Pandey S. 1978. "Population Improvement and Varietal Development in CIMMYT's Maize Program." In Proceedings of XVth Annual Meeting of Caribbean Food Crops Society.



CENTRO INTERNACIONAL DE MEJORAMIENTO DE MAIZ Y TRIGO
INTERNATIONAL MAIZE AND WHEAT IMPROVEMENT CENTER
Londres 40, Apdo. Postal 6-641, México 6, D.F., México