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RECURRENT SELECTION FOR POPULATION, VARIETY, AND HYBRID IMPROVEMENT IN TROPICAL MAIZE

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I. INTRODUCTION

Maize (Zea mays L.) was first used as a source of food by ancient American Indian civilizations, and it also played an important role in their culture. They were responsible for its early domestication and cultivation. Today, maize has become one of the leading agricultural crops and is used for food, feed, fuel, and fiber in many parts of the world, not only in temperate regions but also in tropical and subtropical areas. Much has been written about maize research and production in temperate regions; far less has been written about tropical maize. Recurrent selection theory was developed primarily in the USA and many papers have been published on its application for the improvement of maize populations in the USA Corn Belt and other temperate regions. Much less has been written about its use for the improvement of tropical and subtropical maize.

The International Center for Maize and Wheat Improvement (CIMMYT) was established Apr. 12, 1966 to increase quantity and quality of maize and wheat and alleviate hunger in developing countries of the world. Its center of operations is at El Batan, just outside of Mexico City, but its outreach spans the globe with major programs in Latin America, Africa, and Asia. Over 9 million ha of the world's maize crop are now seeded to CIMMYT-related varieties and there is solid evidence of increasing utilization of CIMMYT germplasm in national programs in tropical and subtropical countries, and even in temperate regions. The heart of the CIMMYT maize program has been recurrent selection at the population level. No other organization has done recurrent selection on such a large scale over such a long period of time. For this reason, CIMMYT maize breeding work will be highlighted in this paper on recurrent selection in tropical maize.

The objectives of this paper are to: 1) discuss tropical maize germplasm and environments in which maize is grown, 2) provide information on recurrent selection systems and how they are applied by the breeder, 3) review maize population improvement work in national programs in tropical regions, 4) highlight recurrent selection work of CIMMYT, and 5) relate population improvement work to hybrid programs for the tropics.

A. THE STATUS OF MAIZE

Maize is grown from 58° N to 40° S in latitude, from sea level to 3,808 meters above sea level (masl), and under 25.4 cm to 1,016 cm rainfall (Hallauer and Miranda, maize in the year 1986. The developing countries produced 40% of the total in about 64% of the total maize area. The developed countries produced 47% of the total in 26% of the area. The remaining area and production occurred in Russia and Eastern Europe. Since the early 1960s, annual maize production in developing countries has been increasing faster (4% per year) than in developed countries (3% per year). Maize yields have increased by 2.8% per year (45 kg/ha/yr) in the developing countries and by 2.4% annually (104 kg/ha/yr) in the developed countries. The average maize yield for the developing countries is about 2.2 t/ha compared to 6.2 t/ha for the developed countries. Developing countries imported about 11 million tons of maize during the period 1986-88, where maize use per capita grew by 1.8% per year, compared to 1.2 % increase in per capita consumption in the developed countries during the same years. Approximately 53% of the maize area in the developing countries is planted to improved maize -- 39% with hybrid seed and 14% with open-pollinated cultivars (OPVs)(CIMMYT, 1987, 1990).

B. UTILIZATION OF MAIZE

About 66% of the maize produced in the world is used as feed, 25% as food and as industrial products, and the remaining is used as seed or is lost. While 20% of the world's maize is used as food in developing countries, only 7% of the maize is used as food in developed countries. Use of maize as feed generally increases with increases in per capita income in developing countries (CIMMYT, 1984).

Maize is a staple food for several hundred million people in Latin America, Asia, and Africa. It provides 15% of the world's annual protein produced from food crops and represents 19% of the world's food calories. Per capita consumption of maize in Mexico, Guatemala, Honduras, Kenya, Malawi, Zambia, and Zimbabwe is about 100 kg per year and in Nepal and the Philippines about 40 kg per year (National Research Council, 1988).

Maize is consumed in many different ways around the world. Its principal use in Mexico and some Central American countries is as tortillas, an unleavened bread made from the dough of de-hulled kernels. In the Andean highlands, maize is mainly used as green ears (choclos). Large seeded, soft (floury) and semi-soft (morocho) maize types are used for this purpose, as well as for preparing 'kancha', 'mote', and a drink, 'chicha'. In the lowlands of the Andean countries, maize is generally used as a compact small bread, named 'arepa'. In Eastern and Southern Africa, maize is used as thick porridge, in West Africa as 'kenkey', and in Asia, cracked maize is usually cooked and eaten like rice or as bread. Maize is also used in soups and broths throughout the world. Maize based products such as corn flour, thickenings and paste, syrups, soft drinks, candies, chewing gums, corn flakes, maize grits, beer, and other alcoholic beverages, are available on store shelves throughout the developing and the developed world (CIMMYT, 1984).

C. TROPICAL MAIZE ENVIRONMENTS

Approximately 60 million ha of maize are grown in the tropics with an average yield of 1.2 t/ha (Brewbaker, 1985). Approximately 42% of all maize grown in developing countries lies in the tropics (Edmeades et al., 1989). Maize yields are primarily limited in the tropics by intercepted radiation to heat unit ratio. The ratio is much lower in the lowlands compared to high altitudes and is lower in the tropics compared to temperate latitudes (G. Edmeades, 1991, personal communication). Relatively less light is intercepted during the rainy season in the tropics which coincides with the grain filling period of the crop. Light interception is further reduced by lower plant densities. Extreme weather variations, erratic rainfalls, high temperatures, particularly during nights, and low temperatures at high altitudes also reduce yields.

Low fertility of most tropical soils reduces maize yields. Nitrogen (N) is the most limiting nutrient in the tropics and provides the major difference between low and high input agriculture. Phosphorus (P) is the second most limiting nutrient and is immobilized by aluminum (Al) and iron (Fe) in acid soils and by calcium (Ca) and magnesium (Mg) in the calcareous soils. The vast majority of tropical soils are acid and Al toxicity is the most important reason for crop failure in such soils (Brewbaker, 1985).

Maize cultivars yield less in the tropics than temperate cultivars in their environments due to their lower grain yield potential. The morphological characters, such as height and leafiness, which might have been important for the adaptation of maize to the tropical environment mean that a considerable portion of the increase in growth brought about by improved management goes to non-grain plant parts (lower harvest index) in tropical maize. Extensive growth in height also contributes to yield losses through lodging.

High pest pressures and suboptimum moisture supply reduce maize yields in the tropics. Diseases frequently reduce production by 30-40% and insects can reduce yields by 100%. Weeds account for 50% of yield losses in the low input agriculture of the tropics (Brewbaker, 1985). Edmeades _et_ _al_. (1989) estimated that less than 5% of maize area in the tropics was irrigated. Average annual yield losses from moisture stress in the tropics were estimated to be: 0-10% in rarely stressed areas, 10-25% in occasionally stressed areas, and 25-50% in the commonly stressed areas. Poor crop management procedures, limited resources, application of inadequate and improper inputs, and a lag in technology transfer, all contribute to reduced maize yields in the tropics.

II. TROPICAL MAIZE GERMPLASM

A. EXTENT OF GENETIC DIVERSITY

Maize seems to have originated in Mexico and was domesticated some 7,000 to 10,000 years ago in south-central or southwestern Mexico (Goodman, 1988). Four major hypotheses have been advanced over the years relating to origin of maize (Hallauer and Miranda, 1988):

1. Maize evolved from a now extinct ancestor native to highlands of Mexico or Guatemala (Weatherwax, 1955).

2. Maize evolved from a cross between <u>Coix</u> spp., and sorghum, perhaps in southwestern Asia (Anderson, 1945).

3. Maize evolved from teosinte directly as a result of human selection (Beadle, 1939).

4. Wild maize was a form of pod corn native to lowlands of South America and modern maize arose from crosses between maize and teosinte or <u>Tripsacum</u> spp., (Mangelsdorf and Reeves, 1939).

Goodman (1988) thoroughly reviewed the available literature, and concluded: (1) that maize either originated as a result of a single evolutionary event that occurred very long ago involving only a few plants that caused the divergence between maize and annual Mexican teosintes; (2) that a single large population of teosinte was converted into maize; (3) that different populations of teosinte gave rise to various maize populations; (4) that maize or annual Mexican teosinte arose as a single or a few plants and acquired over time its cytological, enzymatic, and morphological variability by mutations and backcrossing to the parental taxon. He stated, however, that these hypotheses were not supported by the available archeological and biosystematic evidences.

Anderson and Cutler (1942) proposed the need for a natural classification of the available variability present in maize germplasm and developed the concept of races of maize. They defined a race as a "group of related individuals with enough characteristics in common to permit their recognition as a group, -- in genetical terms it is a group with a significant number of genes in common". The classification of genetic variability in maize of Asia, and Africa is not as advanced as that of Latin America (Goodman and Brown, 1988). A total of 285 races have been described in the Western Hemisphere. Approximately 265 are present in Latin America, the majority in South America. A closer and more critical look at the races, however, suggests that there may in fact be only about 130 distinct races in the Western Hemisphere (Hallauer and Miranda, 1988). Approximately 50% of these races are adapted to 0-1,000 masl, 10% to 1,000-2,000 masl, and the rest to higher altitudes. About 40% of the races have floury endosperm, 30% are flints, 20% dents, 10% popcorns, and 3% sweetcorns (Paterniani and Goodman, 1977). Direct selections from most of these races are presently grown on most of the area planted to maize in the developing world. Migration of original and later users of maize; isolation facilitated by geography, flowering differences, and gametophytic factors; mutations; cross-pollination; natural and artificial selection for preferred grain and ear traits, etc., have all contributed to the creation of a large amount of genetic variability in maize (Hallauer and Miranda, 1988).

Goodman and Brown (1988) summarized the most important characteristics and the heterotic patterns of major racial groups and races. Tuxpeno, a Mexican Dent, is reported to combine well with Coastal Tropical Flints, the race Tuson, and Cuban Flints. Tuxpeno has good stalk quality and tolerance to <u>Bipolaris</u> spp., but it has high ear placement, poor root system, and is susceptible to sugarcane mosaic virus. Tuson has excellent ear type, good grain quality, shorter plants, and tolerance to sugarcane mosaic virus and combines well with Tuxpeno, Cuban Flints, and Chandelle. Coastal Tropical Flints possess excellent grain quality, good husk cover, stalk quality, good roots, and resistance to <u>Bipolaris</u> spp., and are included in such widely used maize cultivars as 'Suwan 1', 'ETO', 'Metro', 'Venezuela 1', and 'Mayorbela'. The racial complex known as Cuban Flints in the Caribbean Islands, Cateto in Brazil, and Argentine Flint in Argentina combine well with Tuson, Tuxpeno, and Coastal Tropical Flints. Their greatest weakness is their susceptibility to virus diseases. Chandelle is an excellent source of prolificacy, low ear placement, and virus resistance but has poor roots. It combines well with Coastal Tropical Flints and Haitian Yellow. The race Haitian Yellow is similar to Coastal Tropical Flints but is late in maturity.

Crossa et al. (1990a) reported on evaluations of diallel crosses among 25 Mexican races, evaluated during 1963 and 1964 at high (2,249 masl) and medium (1,800 masl) elevations, and during 1961 at a lower (1,300 masl) elevation in Mexico. The races Conico, Conico Norteno, and Chalqueno had higher mean yields per se and in crosses at high elevations. Cacahuacintle and Maiz Dulce showed higher cross performance but lower per se yields. Comiteco, Harinoso de Ocho, Celaya, Maiz Dulce, Tabloncillo, and Tuxpeno had higher per se yields and cross performances at intermediate elevations. Highest yields were exhibited by Harinoso de Ocho, Celaya, Tabloncillo, and Pepitilla at lower elevations. Races

Cacahuacintle, Maiz Dulce, and Harinoso de Ocho were the best general combiners across environments.

Estimates vary, but a relatively small proportion of genetic variability available in tropical maize is being utilized by maize breeders and serious efforts for promoting its use have only just begun (R. Sevilla, 1990, personal communication). Many national programs, International Board of Plant Genetic Resources (IBPGR), Latin American Maize Program (LAMP), North Carolina State University, CIMMYT (Vasal and Taba, 1988), and some other programs and groups are directing their efforts to collection, preservation, regeneration, evaluation, and utilization of maize germplasm. These efforts should prove to be of incalculable value to the present and future maize breeders of the world.

B. UTILIZATION OF GENETIC DIVERSITY

Most of the currently available superior maize cultivars and hybrids in the tropics trace their origin to selections from the collections now present in various germplasm banks. However, some of the collections in gene banks may not have been thoroughly evaluated, if at all. Available maize collections could be evaluated at several sites in replicated plots in the general areas of their adaptation. Choice of environments should be such that characterization of the germplasm for major traits of interest and importance to the breeders is possible. Currently grown cultivars should be included as checks in the evaluation trials to provide a measure of problems and potentials of the accessions. Most bank accessions are inferior to currently grown cultivars in most major agronomic traits and, therefore, are increasingly difficult to utilize.

The selected bank collections can be utilized in several ways. Crossa _et_ _al_. (1990a) suggested use of collections to develop new heterotic populations for improvement through reciprocal recurrent selection (RRS), to develop lines and hybrids based on their combining ability, or to introgress them into heterotic populations. The collections or the populations developed by crossing them can also be improved through intrapopulation improvement procedures for development of superior OPVs.

Few accessions have been found usable directly. At CIMMYT, the selected collections are crossed to already agronomically superior populations, and after two cycles of intermating, the resulting populations are improved through recurrent selection. CIMMYT has also systematically introgressed many bank accessions into its broad-based gene pools, which were improved using a modification of modified ear-to-row (MER) selection scheme (CIMMYT, 1979, 1981). The procedure involved planting pre-evaluated and selected accessions as females in the appropriate gene pools. This avoided the possibility of unproven materials contaminating the pool and provided the opportunity for the comparison of the accessions being crossed to the pool. The superior progenies were harvested and their seed was again planted as female rows in the next cycle to obtain an indication of combining ability of the accessions with the pool. Promising accessions thus identified were incorporated in the pool the next cycle, using either remnant seed or seed of the crosses with the pool. Methodology for developing new populations using bank accessions and other materials is described later.

C. MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERISTICS

Paterniani (1990) reviewed the plant characteristics that distinguish maize in the tropics from that in the temperate areas. Tropical maize generally has taller plants, larger tassels, tighter husks, larger leaves, and a greater density of leaf area than its temperate counterparts of equivalent maturity. Tropical maize has lower harvest index (0.30-0.40) compared with temperate maize (0.50-0.55). This difference in harvest index (grain dry weight/total above ground crop dry weight) is associated with differences in morphology between the two groups of germplasm. Tropical maize is also more sensitive to reduced photosynthesis per plant at flowering than temperate maize and is generally highly photoperiod sensitive (G. Edmeades, 1991, personal communication).

III. TROPICAL MAIZE IMPROVEMENT IN NATIONAL PROGRAMS

A. SURVEY OF NATIONAL PROGRAM OBJECTIVES

We conducted a survey of forty-eight maize scientists from the developing countries in Latin America (24), Asia (15), Africa (5), and the Middle East (4) to determine what traits they considered important in their research programs. Ninety-six percent of the scientists considered yield improvement to be an important objective and devoted about 46% of their resources to it (Table I). Sixty-seven percent of those sampled were involved in breeding for disease resistance and devoted nearly 13% of their resources to it. Other traits that were considered important by the breeders were reduced plant and ear height, early maturity, drought tolerance, and grain type, in that order. Lodging resistance, insect and cold tolerance, photosynthetic efficiency, tassel size, stability, protein quality, plant type, prolificacy, etc., were considered important by some but only 2% of the efforts were devoted to these traits.

Table I.

Percentage of efforts that tropical maize breeders devote to different traits and percentage of breeders involved in improvement of those traits. Results based on survey of 48 maize scientists from Latin America, Asia, the Middle East, and Africa.

Traits	Efforts	Breeders involved
	-----------%	-----------
1. Yield	46.4	96
2. Disease Resistance	12.7	67
3. Reduced Plant/Ear Height	8.2	63
4. Early Maturity	8.7	44
5. Drought Tolerance	4.9	29
6. Grain type	3.8	42
8. Other	2.0	18

Yield was the most important trait across the four continents. The next most important traits were maturity and grain type in the Middle East, diseases and drought in Africa, diseases and maturity in Asia, and height and diseases in Latin America. Some attention was devoted to quality traits in Asia and to insect resistance in Africa.

Sprague (1974) and Miranda (1985) advised maize breeders to use different strategies in developing superior cultivars for their farmers, depending on the level of development of the national programs, human and other resources available for research, and capabilities of farmers for effectively using them. Development of OPVs instead of hybrids was suggested for the developing areas. For intermediate areas, breeding programs that introduce and evaluate germplasm sources, followed by population improvement and hybrid development would be advisable. In the developed areas, breeding should involve development and improvement of base populations followed by development of inbred lines and hybrids from the improved populations.

B. MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS

Paterniani (1990) reviewed research conducted in the tropics on the improvement of morphological traits. Reduced plant and ear height is desirable. Paterniani (1990) compared recurrent selection with use of the brachytic-2 gene to reduce plant height and found that both systems were effective. He noted, however, that in using the brachytic-2 approach, recurrent selection would also need to be practiced to adjust the genetic background represented by the modifiers.

Tropical maize cultivars have large tassel size (25-35 branches) compared to temperate cultivars (10-12 branches) and the number of tassel branches has been reported to be negatively correlated with yield, particularly in stress environments (Paterniani, 1990). In Brazil, the brachytic 'Piranao VD-2' population was mass selected for fewer tassel branches for two cycles. About 60% of the plants with large tassel were detasseled before pollen-shed. The next cycle was planted with seed from nondetasseled plants. A 20% reduction in tassel branch number was obtained after two cycles of selection. While the cycles did not differ in yield under favorable environments, the selected population yielded 12% more than C0 under drought and had lower plant and ear height as well. Greater synchronization between male and female flowering are reported to contribute to greater drought tolerance.

C. DROUGHT TOLERANCE

Palacios identified the trait "latente" in the line 'Michoacan 21 Comp 1-104' in 1957 (Molina, 1980; Munoz, et al., 1983). The plants with the trait stop or markedly slow down their development under water stress and resume growth when moisture is supplied. Miranda (1982) observed involvement of the latente gene in tolerance to heat, drought, and frost in maize. In crosses to Tuxpeno, the gene segregated 3:1 and in crosses to Cateto the gene segregated 15:1. He found the latente trait to be recessive and controlled by two genes. Brunini et al. (1985) reported that latente (*lt*) influences stomatal activity, markedly reducing evapotranspiration during water stress. No one, however, has reported successful use of these genes in developing drought tolerant cultivars.

In Mexico, Molina (1980) practiced stratified visual mass selection (MS) for yield under drought to improve drought tolerance in 'Zacatecas 58', 'Criollo del Mezquital', and 'Cafime'. The gains varied with germplasm, years of evaluation, and with level of water stress in the trials and averaged 6.8% per cycle. He concluded that mass selection based on yield under drought was effective in improving drought tolerance in maize. Mashingaidze (1984) evaluated eight genetically diverse lines in diallel crosses for seed germination, seedling recovery, and grain yield under moisture stress. He found greater general combining ability (GCA) effects than specific combining ability (SCA) effects for the three traits. The high SCA effects generally occurred in higher yielding crosses where at least one of the parents had high GCA. Significant maternal effects were detected for seed germination. He concluded that simple selection techniques should be effective in increasing drought tolerance in maize.

D. COLD TOLERANCE

Improving cold tolerance is an important objective for breeders serving the needs of maize farmers in the tropical highlands as well as in winter maize grown in some subtropical areas. Miederna (1979) reported that CIMMYT's Pool-4 ('Highland Early Yellow Flint') and Pool-5 ('Highland Early Yellow Dent') were good sources of resistance to cold temperatures. Hardacre and Eagles (1980) reported on the capacity of autotrophic growth at

13° C in CIMMYT Pool-5 and 'Criollo de Toluca' from Mexico and 'San Geronimo', 'Hurancavelicano', and 'Confite Puneno' from Peru. Khera <u>et</u> <u>al</u>. (1981) evaluated 96 diverse materials for yellowing (chlorosis and bands induced by chilling), purpling, and early vigour in relation to grain yield. The high-yielding families had lower yellowing, higher purpling, and higher early vigour rating compared to the low-yielding families. In another study, Khera <u>et</u> <u>al</u>. (1988) reported that C3 of the population 'Pratap', selected for cold tolerance, yielded higher than C0 (8.23 vs. 7.45 t/ha), had lower leaf yellowing rating (3.8 vs. 4.5), and superior early vigour rating (3.2 vs. 3.5), averaged over 10 trials.

Hardacre <u>et</u> <u>al</u>. (1990) evaluated three maize populations for frost tolerance under temperatures ranging between -1.5 and -5.0° C. Leaf damage and chlorophyll concentrations were assessed at 7 and 28 days after the treatments. Significant and consistent differences were observed for frost tolerance across the populations and the greatest level of tolerance was observed in the hybrid NZ1A x 5-113, derived from CIMMYT's Pool 5, based on materials from the highlands of Mexico. Paterniani (1990) reported on the effect of four cycles of MS in the population 'ESALQ-VD-2' for cold tolerance, after *ABP1* genes for purple color were incorporated into the population. The selected population yielded 7.7% higher than C0 in the winter and 2.4% lower during the summer. The selected population outyielded the commercial hybrids by 2.5-9.8% in the winter. Purple plants were reported to be superior to both green and dark purple plants under cold conditions. Purple plants have been shown to have 0.5 to 3.5° C higher temperature than green plants (Greenblat, 1968). Inside the stalk, purple plants had 1.2 and 1.8° C higher temperatures than green plants at 1.0 and 0.5 cm depth, respectively (Chong and Brawn, 1969).

E. MAIZE DISEASES AND INSECTS

At least 40 significant diseases and as many insects that affect maize are reported in the tropics (Brewbaker, 1984). Maize diseases reduce world's annual maize production by 7-17% (Payak and Sharma, 1985) and only rare maize fields lose less than 5% of their production to pests and diseases. The diseases that significantly suppress yield in the tropics are stunt, streak, downy mildew, and stalk rots (Renfro, 1985). Research conducted with the major maize diseases will be discussed.

1. Downy mildews:

Nine species of fungi are known to cause the disease in maize (Safeeulla, 1975). Resistance to Philippine downy mildew (*Peronosclerospora philippinensis* (Weston) Shaw) has been reported to be polygenic and of threshold type in mature plants. Genes for resistance to this species have been shown to be additive with partial to complete dominance at approximately 50% infection, however, under severe disease pressure, this resistance breaks down and the plants are susceptible (Kaneko and Aday, 1980). Resistance to sugar cane downy mildew (*P. sacchari* (Miyake) Shirai and Hara) has been reported to be generally monogenic with possible existence of polygenic effects (Chang, 1972). Resistance to Java downy mildew (*P. maydis* (Racib.) Shaw) has been reported to be quantitative (Hakim and Dhalan (1973). Brown stripe downy mildew (*Sclerophthora rayssiae* var. *zeae* Payak and Renfro) was reported to be under control of both additive and nonadditive gene effects (Handoo *et al*., 1970). Resistance to sorghum downy mildew (*P. sorghi* (Weston and Uppal) Shaw) was found to be polygenic with additive genetic variance of major importance and dominance and additive x additive type of epistasis of minor importance (Jinahyon, 1973; Singburaudom and Renfro, 1982; Borges, 1987). Resistance is the most efficient, effective, and economical means of control, and resistance to one species of Peronosclerospora has proven useful against other species as well (Frederiksen and Renfro, 1977).

2. Stunt Disease:

Corn stunt is one of the most important biological stresses affecting maize productivity in Latin America (Bajet and Renfro, 1989). The disease is more prevalent in warm humid environments, but it is not restricted to such environments. The pathogen is transmitted by five leafhopper vectors and the geographical range of the disease coincides with that of its vectors (Renfro and Ullstrup, 1976). Two distinct types of corn stunt disease have been identified (Bascope, 1977; Nault, 1980):

1. The Rio Grande corn stunt, now simply known as corn stunt, caused by Spiroplasma kunkelii , or corn stunt spiroplasma, a helical, motile mycoplasma, and

2. The Mesa Central corn stunt, now simply called maize bushy stunt, caused by the maize bush stunt mycoplasma, a nonhelical or pleiomorphic mycoplasma.

3. Streak Virus:

Except for a few reports from some states of India, maize streak virus (MSV) is restricted to Africa and surrounding islands (Seth and Singh, 1975). The disease is considered one of the most important maize diseases in sub-Saharan Africa. It occurs both in the forest and savanna zones and from sea level up to 1800 masl. The magnitude of yield loss varies from season to season and depends on the percentage of infected plants and growth stage at the time of infection. Yield losses of up to 100% have been measured in experiments conducted at the International Institute of Tropical Agriculture in Nigeria (IITA), under artificial streak epiphytotics.

Reliable methods for mass rearing of the vector (Cicadulina spp.) and for the screening of a large number of genotypes have been developed at IITA (Dabrowski, 1987). Kim et al. (1982) reported that 55% of the total variation for disease reaction was due to additive effects, 26% due to nonadditive effects, and 19% due to environmental effects. They calculated that 2 to 3 genes controlled resistance to the disease. The symptoms vary with the genetic background of the susceptible parent and simple recurrent selection or modified backcrossing method has been recommended for breeding for tolerance to the disease (Kim et al., 1989). A single major gene with modifiers was reported by Storey and Howland (1967) and a system of three genes with modifiers was reported by Bjarnason (1986). Excellent sources of resistance to the disease have been developed through backcrossing by many national programs and S_1 selection is being used effectively by CIMMYT in improving resistance (Short *et al*., 1990). Several lines resistant to MSV are available from IITA (Kim *et al*., 1987).

4. Stalk rots:

Diplodia, Gibberella, and Fusarium stalk rots, caused by *D*. *maydis* (Berk) Sacc., *G*. *roseum* f. sp. *cerealis* (Cke.). & Hans, and *F*. *moniliforme*, respectively, cause premature death of plants and contribute to stalk lodging. Any form of stress makes the plants more susceptible to the pathogens. Plants infected by these and Cephalosporium, Colletotrichum anthracnose, and Macrophomina charcoal stalk rots are conspicuous a couple of weeks before physiological maturity. The stalk rots caused by *Pythium aphanidermatum*, *Erwinia chrysanthemi* pv. *zeae*, and *Pseudomonas lapsa* occur during the active growing stage of the plant. Payak and Renfro (1966) reported that stalk rot caused by *C*. *acremonium* was a serious disease in all the maize growing areas of India. Diplodia and Gibberella stalk rots are probably the most destructive seedborne stalk rots in the world (B.L. Renfro, 1985, Personal communication). Bacterial stalk rots (*E. chrysanthemi* Burkholder, McFadden and Dimock and *P. lapsa* (Ark) Starr & Burkh) are important in the hot and humid tropics (Renfro and Ullstrup, 1976). Irrigation with sewage water, a practice common in the tropics, is known to increase the incidence of these diseases.

Khan and Paliwal (1980) observed that GCA effects were more important than SCA effects for resistance to *C. acremonium* and that resistance was partially dominant over susceptibility. While qualitative inheritance has been reported for the bacterial stalk rot (Singh, 1979), additive gene effects have been reported for Pythium stalk rots (Diwakar and Payak, 1975). Resistance to Diplodia stalk rots involves additive gene action and genes for resistance have also been located on various arms of several chromosomes. Resistance to Fusarium stalk rot appears to be qualitative (Hooker, 1978). Younis *et al*. (1969) reported that resistance to stalk rot caused by *F. moniliforme* was dominant over susceptibility. Presence of the "stay green" trait has been associated with tolerance to stalk rot (De Leon and Pandey, 1989).

5. Ear rots:

Ear rots of maize in the tropics are usually caused by _D_. _maydis_, _Rhizoctonia_ _zeae_ Voorhees, and _F_. _moniliforme_. Diplodia ear rot is more common in the warmer and more humid areas. Cultivars with loose husks, exposed ear tips, and upright ears show more susceptibility to the disease. Grains infected with _F_. _moniliforme_ are reported to be toxic and cancerous to animals. Inheritance studies for resistance to most ear-rot-causing pathogens indicate it to be polygenic with generally additive effects. Resistance of inbred lines has been found to be a poor indicator of the tolerance in hybrids (Renfro, 1985).

Ear rots are also caused by _Aspergillus_ _flavus_ and _A_. _parasiticus_ in maize, particularly in hot and humid environments. Although, the disease is generally considered a storage disease, field infection does occur. _A_. _flavus_ requires at least 17.5% moisture and between 28° and 35° C temperature for optimum growth (Diener and Davis, 1987). The fungi produce aflatoxins that have many effects on farm animals including malabsorption of nutrients, coagulopathy, decreased tissue integrity, poor growth, increased susceptibility to diseases, medicine failures, and reduced reproductive potential (Hamilton, 1987). In mammals, they cause hepatic necrosis, coagulopathy, and death: they are considered a hazard to public health (Pier, 1987). The same environmental factors that influence aflatoxin production in storage also affect levels of field infection. Insects, particularly *Sitophilus zeamais* Motschulsky, increase kernel infection with *A. flavus* (McMillian, 1987). Significant differences have been reported for resistance among genotypes and primarily additive genetic variation has been observed for resistance to *A. flavus*. Recurrent selection has been suggested to increase the level of resistance (Widstrom, 1987).

6. Leaf diseases:

Leaf diseases are of lesser importance than 10 years ago because newer cultivars are more tolerant to the diseases (Renfro, 1985). Northern leaf blight (*Exserohilum turcicum* (Pass.) Leonard and Suggs) is usually present at higher altitudes in the tropics. Resistance is both polygenic and qualitative in nature. Southern leaf blight (*B. maydis*) is very destructive in the tropics. Three races (O, T, and C) of the pathogen have been identified (C.De Leon, 1991, personal communication). Both monogenic and polygenic resistances are known but even in the polygenic system, few genes are involved (Renfro, 1985). Faluyi and Olorde (1984) reported resistance to B. maydis to be monogenic recessive in their studies based on resistant varieties 'RbU-W' and 'DIC'. Curvularia leaf spot is widely distributed in the tropics and is caused by Curvularia lunata (Wakker) Boed. While it causes only moderate damage to leaves, in certain areas the disease may become severe (Renfro and Ullstrup, 1976). Vasal et al. (1970) estimated that up to 15 genes might be involved in resistance and both additive and epistatic effects were important.

Two types of rusts, common (Puccinia sorghi) and southern (P. polysora), are known to be important. Both quantitative and qualitative systems are known to govern the resistance to the two diseases. Five loci have been identified which condition resistance to common rust and 11 loci to southern rust (Renfro, 1985). A single complex locus (*Rpl*) identified in the 'Cuzco' variety of Peru has provided resistance to many cultures of P. sorghi (Hooker and Le Roux, 1967).

7. Insect resistance:

Insects destroy approximately 12% of the world's maize production annually (Cramer, 1967). Stem borers, represented by different genera in tropical America, Asia, and Africa, the *Spodoptera* budworms, the *Heliothis* earworms, and the stored grain insects are considered to be the most important insect pests of maize. Four borers are known to cause significant yield losses in Africa: the pink stalk borer (*Sesamia calamistis* Hmps.), the African sugarcane borer (*Eldana saccharina* Walker), the maize stalk borer (*Busseola fusca* Fuller), and the spotted stalk borer (*Chilo partellus* Swinhoe). While the first three are known to be present only in Africa, *Chilo* appears to have been recently introduced into East Africa from Asia. The borers can cause yield loss of 10-100% in Africa (Usua, 1986). Yield losses to *C. partellus* have been reported to be up to 18% in Kenya and 44% in Pakistan.

Breeding for tolerance to *S. calamistis* was less effective as compared to that for *E. saccharina*. (Bosque-Perez *et al*., 1989). Resistance to *Chilo* has been reported by Chatterji *et al*. (1971) and Ampofo *et al*. (1986). Sarup (1980) proposed half-sib (HS) recurrent selection for improving tolerance to *C. partellus* in maize and reported on use of modified full-sib (FS) selection scheme to develop *Chilo* tolerant experimental varieties. Recurrent selection under artificial infestation has been recommended by Ampofo and Saxena

(1989) for development of cultivars resistant to *Chilo*. Omolo (1983) evaluated lines received from CIMMYT for their tolerance to this insect. He found several families from populations 25 and 27, previously selected for tolerance to sugarcane borrer (SCB) (*Diatraea saccharalis*) (a few also were selected for tolerance to *Ostrinia nubilallis* and South-western cornborer (SWCB) (*D. grandiosella*) were also resistant to *Chilo*. He suggested that crosses between local African maizes and exotic Mexican materials should offer multiple resistance or multiline approach to pest management.

While breeders in the past were largely unsuccessful in developing genotypes resistant to *B. fusca*, recent efforts seem more promising. Although no maize germplasm is immune to the insect, several materials have shown intermediate levels of resistance to the first generation (whorl feeding) larvae. Resistance appears to be additive and efforts to transfer the trait through backcrossing have generally been unsuccessful, due mainly to nature of resistance (Barrow, 1989).

Williams and Davis (1989) reported on performance of eight maize lines under artificial infestation with 30 larvae of SWCB and *Spodoptera frugiperda* (FAW). While the leaf feeding rating for SWCB for the susceptible check was 9.0 (rated on a scale of 1-9, where 1 = immune and 9 = highly susceptible), the lines ranged from 4.5 to 6.5. In another study, GCA was the only significant source of variation for leaf feeding by SWCB but both GCA and SCA were important for larval growth on maize calli in the same trial (William and Davis, 1985). Williams and Davis (1990) artificially infested a maize hybrid with 30 FAW and 30 SWCB larvae at the whorl stage to determine relative differences in the damage caused by the two insects. While both insects caused extensive feeding damage, only SWCB caused 50% reduction in ear height. Yield reduction caused by FAW was 13% compared with 57% with SWCB infestation.

In the study of Williams and Davis (1989), the susceptible check averaged 9.0 for FAW leaf feeding and the lines ranged between 5.5 and 7.0. In a diallel trial of nine lines, Williams et al. (1978) reported that both GCA and SCA effects were important sources of variation for resistance to FAW. Most materials with higher levels of resistance to FAW contain Antigua germplasm. Two cycles of S_1 selection reduced leaf feeding by 3.5% per cycle while MS was ineffective in improving the trait. Heritability estimates for resistance range between 12-45% for leaf feeding, and leaf feeding is positively correlated with yield losses (Widstrom, 1989).

Ear tip invading insects are among the most destructive maize pests in the world. They are responsible for up to 4% losses in field maize, 14% in sweet corn in the U.S.A., and higher losses in the tropics (Brewbaker and Kim, 1979). Tropical lowland maize races and composites have resistance to ear pests due mainly to high number of husks tightly covering the ear tip. Tropical highland germplasm, on the other hand, has a lower number of husks. The Mexican race Zapalote Chico has a high number of tight husks and provides resistance to ear worms (Brewbaker, 1974). Resistance to ear worm in this germplasm may also be due to presence of an antibiotic factor in its silks (Straub and Fairchild, 1970). Waiss et al. (1979) identified this factor to be Maysin, a flavone glycoside, that severely retarded growth of Heliothis zea (Boddie) larvae on maize silks. Highly significant GCA and SCA effects for tolerance, with GCA effects about twice as large as SCA effects, have been reported by Widstrom (1972) and Widstrom and Hamm (1969). Widstrom (1989) suggested use of recurrent selection to build up resistance to H. zea (Boddie) in maize populations. About 3.9% reduction per cycle in ear damage has been reported from HS selection (Widstrom et al., 1970) and 3.5% reduction through S_1 selection based on an index involving husk tightness, husk extension, and maturity (Widstrom et al., 1982).

The maize weevil (*S. zeamais* Motschulsky), often referred to as the rice weevil (*S. oryzae* L.), is an economic pest of maize. Pant *et al*. (1964) evaluated 11 cultivars for their tolerance to maize weevil and found variation among them. Ivbijaro (1981) reported greater tolerance to *S. zeamais* in the Nigerian material TZE 3. Widstrom (1989) suggested that improvement of resistance to maize weevil was seldom included as a breeding objective, although increased husk coverage and tightness reduced damage by the insect. He also reported variation for resistance to weevil damage to be largely additive and obtained a reduction of 3.6 and 5.1% per cycle in two populations involved in a RRS program after two cycles of selection.

F. TOLERANCE TO SOIL ACIDITY

Acid soils cover a significant part of 48 developing countries and involve 1,660 million ha (Table II). About 64% of the land surface of tropical South America, 32% of tropical Asia, and 10% of Central America, Caribbean, and Mexico are considered acid soils (Sanchez, 1977). Over 820 million ha of this land is suitable for crop and pasture production and another 620 million ha for grazing (Overdal and Ackerson, 1972).

Soils are acidic because their parent materials were acidic and initially low in the basic cations (Ca, Mg, potassium, and sodium) or because the elements have been removed from soil by leaching or by the harvested crops. Maize suffers in soils with pH lower than 5.6, due mainly to toxicity from Al and manganese and deficiency of Ca, Mg, P, molybdenum, and Fe. Maximum damage in acid soils is caused by Al toxicity. In mineral soils (<3-4% organic matter), the exchangeable acidity is mostly due to Al; while in soils with higher organic matter, soil acidity may be due to exchangeable hydrogen.

Table II.

Oxisols and ultisols in the tropics (million ha)[a]

	America	Africa	Asia	Total
Forests	555	455	190	1,200
Savannas	205	195	60	460
Total	760	650	250	1,660

[a] Adapted from Sanchez (1977).

Aluminum is the most important cause of yield losses in acid surface soils and it can be precipitated and thus detoxified by liming. However, in areas remote from lime sources or lacking good road systems, on-farm costs of lime may be too high. Even in limed soils, excess soluble or exchangeable Al remains in the sub-soils, as lime does not readily penetrate below the zone of application. Liming subsoils deeper than 30 cm is very difficult and prohibitively expensive. Even in limed soils, acid subsoils may restrict plant roots to surface layers inhibiting their normal formation, thereby reducing nutrient and water uptake and reducing yield. Also lime application must be repeated every few years depending upon the soil conditions.

Genetic tolerance in maize to soil acidity would provide an ecologically clean, energy conserving, and a more sustainable and cheaper solution to the problem than amending soils. Genetic differences for Al tolerance among inbreds, hybrids, and open pollinated populations have been reported (Naspolini _et_ _al_., 1981; Magnavaca, 1983; Magnavaca _et_ _al_., 1987b; Magnavaca _et_ _al_., 1987c). Magnavaca _et_ _al_. (1987a) showed that additive genetic variation was twice as important for Al tolerance as dominance. In a study in nutrient solution involving 11 Brazilian lines and 17 USA lines, Brazilian lines were reported to be more tolerant to Al and had more and longer seminal and adventitious roots than USA lines. Selection for high yield was reported to reduce root length in the population 'Composto Amplo'. When grown under acid soils, a reduction in frequency of highly tolerant plants was accompanied by an increase in intermediate tolerant plants.

Relative net seminal root lengths and the ratio of final seminal root lengths to initial seminal root lengths were best indicators of Al tolerance among maize lines, particularly at relatively high Al concentrations. Evaluation of 50 cultivars in the field indicated that genetic variation existed among them for tolerance to Al and that yield, relative to the mean of the selected entries, would be the best measure of Al tolerance of maize genotypes. Field performance of genotypes was not highly correlated with responses under nutrient solution. However, the correlation was higher at higher levels of Al stress (Kasim, 1989).

IV. RECURRENT SELECTION IN MAIZE

A. RECURRENT SELECTION SYSTEMS

The basic objectives of any recurrent selection system are: 1) to improve breeding populations in a cyclic manner by increasing the frequencies of favorable genes and gene combinations, and 2) to maintain adequate genetic variability for further selection and improvement by intermating a sufficient number of superior genotypes each cycle of selection. Ultimately, these improved populations should be an excellent germplasm resource for direct release to farmers, for the extraction of superior OPVs or for the development of inbred lines for use in new hybrids for farm production.

Recurrent selection systems include all those systems that repeat the same procedure cycle after cycle. The procedure generally involves: 1) production of a set of genotypes (individuals or families of some type), 2) evaluation of those genotypes and identification of superior ones to be used as parents of the next generation, and 3) intermating the selected genotypes to produce the next generation (improved cycle).

The number of years required per cycle of recurrent selection may vary from one to three or more depending upon the system used, and whether or not two growing seasons in a year are available. The evaluation and selection phase should be conducted in environments representative of the target area in which a final product will be released for on-farm production. In the intermating of selected genotypes and/or in the development of new genotypes for evaluation, some visual selection can be practiced for plant type, disease and insect resistance, etc. Visual selection can be done most effectively in the target area, but this may lengthen the selection cycle. Use of second season nurseries not only shortens the selection cycle, but it can also be used for evaluating response to diseases and insects not always present in the target area.

Recurrent selection systems have been discussed extensively in the literature and summaries have been presented by Sprague and Eberhart (1977), Gardner (1978), Hallauer (1985), Hallauer and Miranda (1988), Hallauer et al. (1988), and Paterniani (1990).

Recurrent selection systems are generally divided into two types: 1) Intrapopulation Recurrent Selection Systems, and 2) Interpopulation Reciprocal Recurrent

Selection Systems. Within each system, there is 1) an evaluation unit, and 2) a selection unit. In a few systems, the individual plant is the unit evaluated and the unit selected. In most systems, however, the evaluation unit is some kind of family. The selection unit may be the same family evaluated, but it may also be a related family.

Family evaluation normally requires replicated tests of families in environments representative of the area for which the population is being developed. Experiment station sites are most often used. Selection is based on performance of families evaluated. Superior families in the test or some family related to the selection unit are intermated to form the improved population used for the next cycle of selection.

In most intra- and interpopulation selection schemes, the intermating phase involves making crosses among selected families or their relatives (selection units). This may be done in several ways in a second season nursery or in the main growing season. The simplest procedure is to grow the selected families in female rows to be detasseled in an isolated nursery, and to use a bulk composite of seed from all selected families to plant male rows for the pollen source. If isolations are not available, the diallel cross among all selections can be made but often involves too many crosses; hence, a partial diallel or chain crossing is used where each selection is crossed to the same number of other selections. A balanced composite involving the same number of crossed seeds from each selected family constitutes the improved population used to initiate the next cycle.

In addition to constituting the improved population, intermating selected families also breaks gene linkages and permits genetic recombination to form new genotypes and maintain genetic variability. In some systems, intercrossing selected families and producing new families for testing can be done simultaneously (Compton and Lonnquist, 1982); however, genetic variability and selection limits may be reduced because of less opportunity for genetic recombination. For traits expressed prior to pollination, identification of superior families and intermating them to form new families for testing makes possible completion of a cycle of selection per season. In short-term selection programs, loss of genetic variability may not be serious, and limiting recombination may be desired to retain favorable epistatic gene combinations. However, in long-term programs, maintenance of genetic variability and maximizing selection limits by separating the intermating and the new family production phases are desirable.

B. INTRAPOPULATION RECURRENT SELECTION SYSTEMS

1. MASS SELECTION

a. Simple Mass Selection (MS) is the oldest and simplest of all recurrent selection systems, and was probably used by ancient native cultures for maize improvement. It was certainly used by early farmers, who saved seed ears from high-yielding plants in their fields at harvest time. Early maize breeders thought such a system was ineffective for yield improvement, although it was effective for other traits. Masking effects of soil heterogeneity and unequal competition among plants due to unequal spacing in the field contributed greatly to plant-to-plant variation and overshadowed the contribution of the genotype to individual plant yield. Keen observers, who evaluated each plant in relation to its surrounding neighbors, undoubtedly did make progress with this selection system.

b. Stratified Mass Selection (SMS) was suggested by Gardner (1961) as a simple procedure to control environmental influences on individual plant yield. The selection area is divided into small, approximately square plots within which the soil heterogeneity and other environmental variables are minimal. Selection is restricted to among plants within each plot. Gardner also suggested use of overplanting and adjusting to perfect stands to provide equal competition to all plants, and use of an isolated field to avoid pollen contamination.

c. Stratified Mass Selection with Pollen Control (SMSP) can only be done when selecting for traits that can be evaluated prior to pollination, e.g. days to flower (Troyer and Brown, 1972, 1976) plant and/or ear height, number of leaves, number of shoots (Paterniani, 1978), etc. In maize, all unselected plants are detasseled so that mating occurs only among selected plants. Additional selection for yield among female plants may be done at harvest time.

d. Mass Selection with Genetic Stratification was discussed by Paterniani (1990) who credited Zinsly with the idea; however, the "Screening Honeycomb Design" suggested by Fasoulas (1973, 1977) and Fasoulas and Tsaftaris (1975) is basically the same idea. A constant check genotype is planted systematically throughout the field and individual plants of the selection population are compared to nearest check plants in making selections. To avoid contamination to a maize population undergoing selection, such a check must be: 1) male sterile, 2) detasseled, or 3) possess a trait that makes outcrosses easily identifiable in the seed of selected plants. Since such a system is labor intensive and quite expensive to operate compared to SMS, it has not been widely used.

2. HALF-SIB FAMILY SELECTION

a. Ear-to-Row (ER) selection involves open-pollinated seed of individual plants of a population planted and evaluated in a single HS progeny row with no pollen control (Hopkins, 1899, Montgomery, 1909). Ears from the best plants in the best families are chosen for ear-to-row planting and selection the following cycle. This system was used by plant breeders more than a century ago, but early maize breeders found it to be relatively ineffective for yield improvement but useful for improvement of other highly heritable traits.

b. Modified Ear-to-Row (MER) selection was suggested by Lonnquist (1964) and involves single replication testing in multiple environments with an isolated nursery used for intermating. In the nursery, each HS family is grown and detasseled. Male rows planted from a balanced composite of seed from all HS families are interspersed among the female HS families and provide the pollen source. Selection is done among HS families based on yield performance, and also among plants within HS families based on visual yield potential. Simultaneous yield testing and intermating permits advancement at the rate of a cycle per year.

c. Modified-Modified Ear-to-Row (MMER) selection, used by Paterniani (1967) for one cycle only and described in detail as a system by Compton and Comstock (1976), is based on testing and selection as in the above system. However, intermating is done in a second growing season and only selected HS families are planted as female rows to be detasseled in the isolated nursery, and only selected HS families are included in the balanced bulk composite used to plant the male rows. This system requires two years per cycle. An isolated second season nursery can be used for the recombination phase to reduce cycle time to one year but if the environments are different, within family selection may not be very effective.

d. Half-sib Family evaluation and selection (HS) involves replicated yield testing, preferably in two or more environments as described above, of the progeny of individual plants that have been open pollinated or hand pollinated with a random sample of pollen from the same population (Jenkins, 1940). Selected HS families are intermated the following season. After intermating, a balanced composite of seed from crosses, with each selected family equally represented, is used to form new HS families. This system requires three growing seasons. The intermating phase and the production of new families phase are sometimes combined (Compton and Lonnquist, 1982) in the same season, which reduces cycle time requirement to two growing seasons. One advantage of using HS families is that an estimate of additive genetic variance and of heritability are available each cycle of selection.

3. FULL-SIB FAMILY SELECTION

Full-sib Family evaluation and selection (FS) involves yield testing of the progeny of intrapopulation paired-plant crosses. Testing and intermating are done using methods described above. (Moll and Robinson, 1966). A balanced composite of seed from crosses (each selected parent represented equally) provides the improved cycle from which new FS families are developed for the next cycle. Cycle time is three growing seasons. This system has been used extensively by CIMMYT in the international maize-improvement program as well as by others. By intercrossing selected families and producing new FS families simultaneously, only two growing seasons are required.

4. S_1 FAMILY SELECTION

a. $\underline{S_1\text{ Family Evaluation}}$ per se (S_1) involves yield testing of progenies produced by self-pollination of a number of plants in a population (Eberhart, 1970). Yield testing of progenies and intermating of selected ones is conducted in the same manner as described for all family systems. New families are produced by selfing plants in the balanced composite of the intermated population. Three growing seasons are required.

b. HS (Topcross) Family Evaluation for GCA (S_1HS) involves simultaneous self pollination of an individual plant in a population and topcrossing that same plant to a random sample of plants of a broad-based tester population (Jenkins, 1940). With prolific plants, the first ear can be topcrossed with a pollen-bulk of the tester and the second ear selfed. Topcrossed HS families are evaluated in replicated trials, but the S_1 families related to the best topcrosses in the yield trial are used in the intermating phase. Three growing seasons are required. A modification involves selfing S_0 plants and growing S_1 progenies as females in an isolated topcrossing block with the tester used as male to produce topcrosses. This would require four growing seasons but still two years.

c. FS (Topcross) Family Evaluation for SCA (S_1FS) involves simultaneous self pollination of an individual plant in a population and outcrossing that same plant to an inbred line tester (Hull, 1945, 1952). Topcrossed FS families are tested as described above, but S_1 families related to the best topcrosses are used for the intermating phase. Three growing seasons are required. Although designed originally to develop a source population from which lines could be extracted for use in hybrids with an available elite line, it has worked effectively for population improvement (Horner et al., 1963, 1973; Russell et al., 1973; Russell and Eberhart, 1975).

5. S_2 FAMILY SELECTION

a. S_2 Family Evaluation per se (S_2) involves two generations of self-pollination, which can be done with or without selection in the S_1 generation (Horner et al., 1973). S_2 families are tested and the superior ones selected and intermated as described for other family types. This system requires four growing seasons. Because of large G x E interactions, and difficulties of evaluating inbred maize progenies per se, this system has not been used extensively.

b. FS (Topcross) Family Evaluation for SCA (S_2FS) involves simultaneously selfing S_1 progenies and topcrossing them to an inbred line and yield testing the topcrosses as described for other types of families (Horner et al., 1963). Because the S_1 progenies trace back to a single plant in the population and are crossed to a homozygous line, the cross is basically the offspring of two parents, hence a FS family. For intermating, the S_2 families related to the best topcrosses in the test are used. Four growing seasons are required for each cycle. If selection within the S_1 families to be topcrossed is desired, this can best be done in the target environment and would require three years per cycle. This system can be used for extraction of lines for hybrid development as well as for population improvement.

6. S_n FAMILY SELECTION (SINGLE SEED DESCENT)

a. Inbred Family Evaluation (S_n) involves development of inbred lines (S_n generation) through the single seed descent method (Brim, 1966). Use of two seasons per year greatly accelerates this process. Inbred families are tested in yield trials and the best families are intermated. The number of growing seasons required varies depending upon the number of generations of inbreeding and time required for each.

b. Full-sib (Topcross) Family Evaluation for SCA (S_nFS) involves selfing to near homozygosity before topcrossing to an elite inbred line. Topcrosses are yield tested and selected for SCA. S_n lines related to the superior topcrosses are intermated. Number of growing seasons required depends upon generations of selfing. A variant of this system or of system S_2FS is used on F_2 populations of single crosses or other elite narrow-based populations by most USA commercial maize breeders in developing new lines for hybrids. Cycle length is so long that it is not very useful for broad based population improvement.

C. INTERPOPULATION RECIPROCAL RECURRENT SELECTION SYSTEMS

1. RECIPROCAL HS FAMILY EVALUATION

a. S_1 Family Selection (RRS) was suggested by Comstock et al. (1949) as a breeding system that would permit utilization of all genetic effects in the improvement of the heterotic response in the cross of two populations. Individual plants of population A are each self pollinated and simultaneously crossed to a random sample of plants of the reciprocal population B. Likewise, individual plants of population B are simultaneously self pollinated and crossed to a random sample of plants in population A. A balanced composite of the crossed ears of each plant constitute a HS family. HS families of each population are evaluated in replicated yield trials in multiple environments. S_1 families related to the superior HS families within each population are used for the intermating process to produce the improved cycles of the two reciprocal populations. This system requires three growing seasons per cycle.

Because of high labor involvement and costs of manually making topcrosses plus inadequate sampling (6 to

10 plants) of the tester population in the original scheme, an alternative system described by Paterniani (1990) seems better. It involves selfing individual plants in each population and growing the two sets of S_1 families as females in separate isolation blocks with reciprocal populations used for male rows and border. S_1 families are detasseled and pollinated by the reciprocal population to produce the HS families for testing. Remnant seeds of S_1 families related to superior HS families are used for the recombination. This system takes an additional growing season.

b. <u>HS Family Selection</u> (RHS) suggested by Paterniani (1970) involves use of open-pollinated progenies (HS families) of each population grown in separate isolation blocks where they are detasseled and pollinated by the reciprocal population grown in male rows and in borders. Testcross families are grown in replicated trials and HS families related to the superior testcross families are used for recombination. Within each population, selected HS families are grown as female rows and detasseled in an isolated block and a bulk mixture of seed of selected HS families from the other population is planted in male rows and around the border to provide the pollen source to form new HS families to begin the next cycle and to constitute the improved reciprocal population. Thus the system requires only three growing seasons to complete a cycle. A cycle can be completed in two growing seasons in one year by growing the recombination block and yield trials simultaneously. However, selection will be on the female side only and gains per cycle will be reduced (E. Paterniani, 1991, personal communication).

c. HS Family Selection Using Prolific Plants (RHSP) was also suggested by Paterniani (1970) to reduce the selection cycle to two growing seasons, which could be accomplished in one year with a second season nursery. Two-eared plants are required in each of the two populations. Two isolation blocks are required. In isolation 1, population A is planted in female rows and population B is planted in male rows. In isolation 2, B is female and A is male. At flowering time, female rows are detasseled and the second shoot of prolific female plants is covered with a shoot bag. When bagged shoots are ready to be pollinated, bulk pollen is collected from 50 or more prolific plants being used as males in the other isolation (say isolation 2) and are used to pollinate bagged shoots of that same population in isolation 1. Likewise males in isolation 1 are used to pollinate bagged female shoots in isolation 2. The open-pollinated top ear produces an interpopulation HS family, which is used in replicated yield trials; and the hand-pollinated second ear produces an intrapopulation HS family, which is available to be used simultaneously for recombination and for formation of new inter- and intra-HS families to begin the next cycle. With a second season nursery, a cycle can be completed in one year.

2. RECIPROCAL FULL-SIB FAMILY EVALUATION

a. S_1 Family Selection based on reciprocal plant-to-plant crosses (RFS) requires the use of two-eared plants (Villena, 1965; Lonnquist and Williams, 1967; Hallauer and Eberhart, 1970; Jones et al., 1971). An individual plant in population A is crossed to an individual plant in the reciprocal population B using one of the ears. The reciprocal cross is also made if possible. At the same time the plants are each self-pollinated using the other ear. Selection is based on the cross performance in yield trials, and the S_1 families related to the selected crosses are used for intermating within each of the reciprocal populations. Intermating is often done in an isolated crossing block where S_1 families are detasseled for use as females, and a balanced bulk of seed of all S_1 families is used to plant male rows at intervals in the field and in the border. A balanced composite of seed with equal contributions from each selected family constitutes the completed selection cycle, and this seed is used to initiate the next cycle. Three growing seasons are required per cycle.

b. S_1 Family Selection based on reciprocal S_1 x S_1 family crosses (FSRRS). An alternative procedure is to produce S_1 families in each population and make paired-row crosses between S_1 families from opposing populations (Marquez-Sanchez, 1982). Such S_1 x S_1 crosses are basically a cross between two non-inbred plants as in the above scheme, but prolificacy is not required. These crosses which might be called FS families are evaluated, and S_1 families related to the best crosses are intermated. This lengthens the cycle to four growing seasons.

c. S_1 Family Selection based on reciprocal inbred line testcrosses (MRFS). Russell and Eberhart (1975) suggested a modified FS reciprocal recurrent selection procedure in which noninbred (S_0) plants of population A are each self pollinated and crossed to an inbred line of population B derived from a previous cycle. Likewise noninbred plants of B would be selfed and crossed to a previously derived line from A. Testcross performance would be the selection criteria and S_1 lines related to the best testcrosses would be the selection units. Two elite inbred lines from different heterotic groups, e.g.

B73 and Mo17, that produce an exceptional hybrid might also be used as testers to improve two populations and their interpopulation cross. Testers for each population would be chosen according to heterotic responses noted in the population x tester crosses. Since the tester lines would be homozygous, greater genetic variability would exist among testcross families compared to when populations are used as testers. This suggests that greater progress from selection should be possible using inbred testers; however, Comstock (1979) presents theoretical arguments indicating that populations are slightly superior to inbred lines as testers in shifting gene frequency in directions favorable for increased cross performance.

The units evaluated, selected, and recombined for most of the selection systems discussed are presented in Table III.

Table III.

Recurrent selection systems used for intrapopulation improvement and for the improvement of interpopulation crosses

Populations Improvement Systems	Value of c[a]	Unit Evaluated	Unit Selected and Recombin
INTRAPOPULATION SYSTEMS			
1. Mass selection of individual plants			
a. Simple mass selection (No pollen control)	0.5	Female plant in field	Female open-pollinated seed
b. Stratified mass selection (No pollen control)	0.5	Female plant in restricted area	Female open-pollinated seed
c. Stratified mass selection (Pollen controlled)	1.0	Plant saved prior to pollination	Female open-pollinated seed
d. Mass selection with a constant genotype planted systematically for comparison and evaluation	0.5	Female plant relative to check	Female open-pollinated seed
2. Half-sib family selection			
a. Ear-to-row (No pollen control)	0.125	HS family, no replication	HS family
b. Modified ear-to-row (No pollen control)	0.125[b]	HS family replicated[c]	Plants within selected HS

ble III. Continued.....

pulations Improvement Systems	Value of c[a]	Unit Evaluated	Unit Selected and Recombined
c. Modified-modified ear-to-row (Pollen controlled)	0.25[b]	HS family replicated[c] plants/family in isolated block	Plants within selected HS family with restricted crossing
d. Family evaluation	0.25	HS family replicated	HS family
Full-sib family selection			
a. Family evaluation	0.5	FS family replicated	FS family
S_1 family selection			
a. S_1 family evaluation per se	1.0[d]	S_1 family replicated	S_1 family
b. Half-sib family evaluation (GCA)	[e]	HS (TC) family replicated	S_1 family
c. Full-sib family evaluation (SCA)	[e]	FS (TC) family replicated	S_1 family

Table III. Continued.....

Populations Improvement Systems	Value of c[a]	Unit Evaluated	Unit Selected and Recombined
5. S_2 family selection			
a. S_2 family evaluation per se	1.5[d]	S_2 family replicated	S_2 family
b. Full-sib family evaluation (SCA)	[e]	FS (TC) family replicated	S_2 family
6. Single seed descent			
a. Inbred family evaluation	2.0[d]	S_n family replicated	S_n family
b. Full-sib family evaluation (SCA)	[e]	FS (TC) family replicated	S_n family
INTERPOPULATION SYSTEMS			
1. Reciprocal half-sib family evaluation			
a. S_1 family selection		HS testcross family	S_1 family

ble III. Continued.....

pulations Improvement Systems	Value of c*	Unit Evaluated	Unit Selected and Recombined
b. Half-sib family selection		HS testcross family	HS family
Reciprocal full-sib family evaluation			
a. S_1 family selection			
i) Based on cross to a reciprocal plant		FS testcross family	S_1 family
ii) Based on cross to a homozygous line		FS testcross family	S_1 family
b. Full-sib family selection		FS testcross family	FS family

is the proportion of additive genetic variance contained in the genetic component of variance among selection units.

here is also an additional formula for expected additional gain from within family selection in which c = 3/8 or 0.375.

topcross family evaluation, progress in population improvement depends on the distribution of gene frequencies in the tester (see Empig, et al. 1981).

inbred families, additive genetic variance among families increases to $(1+F)\,\sigma^2_A$ and dominance variance is halved each generation.

D. EXPECTED GENETIC GAINS

For most of the recurrent selection systems discussed, equations to predict progress from selection have been developed. Detailed derivations are given for many systems by Empig _et_ _al_. (1981). Sprague and Eberhart, (1977), Gardner (1978), and Hallauer and Miranda-Fo (1988) summarize prediction equations. For intrapopulation selection, the general prediction equation for expected gain per year is:

$G_s = SH/y = [(k\ \sigma_p)\ c\ \sigma_A^2] / [y\ \sigma_p^2]$

S = selection differential (superiority of the mean of selected units over theσ population mean).

= $k\ \sigma_p$ in normally distributed populations.

k = number of phenotypic standard deviations that selected units are expected to exceed population mean in normally distributed populations.

σ_p^2 = phenotypic variance among selection units.

= MS_f / re, where MS_f = the family mean square, r = No. of replications, e = No. of environments.

σ_A^2 = additive genetic variance in the population.

c = proportion of additive genetic variance contained in the genetic component of variance among selected unit means. Values are given in Table III.

H = $c\sigma_A^2/\sigma_p^2$, heritability on a selection unit basis.

y = number of years per cycle.

Estimates of the magnitude of additive genetic variance in the population and the phenotypic variance among selection unit means are required. Factors affecting gains from selection are the number of selection units evaluated, the proportion selected, the magnitude of additive genetic variance, and the precision of the experiment. Except for HS family evaluation and selection, substitution of the family component of variance for $c\sigma_A^2$ will give biased estimates of expected gain for traits where nonadditive genetic effects are important. Where the units selected differ from those evaluated, estimates of additive genetic covariance between the two types of families are substituted for additive genetic variance.

For reciprocal recurrent selection systems, expected gains in the interpopulation cross are calculated using components of variance among intercross family means (see references listed above).

V. POPULATION FORMATION AND FACTORS AFFECTING CHOICE OF SELECTION METHODS AND PROGRESS FROM SELECTION

In choosing germplasms and forming populations, the ultimate goal and time constraints are important. For intrapopulation selection, the population should possess the most desirable alleles at as many loci as possible. For interpopulation selection, heterotic patterns are of great significance in choosing germplasms to include in each of the two reciprocal populations. There is no lack of maize germplasm available for the formation of breeding populations. Locally adapted material and material from other countries with similar environments will be most useful; however, superior but less well-adapted germplasms from other areas no doubt contain favorable alleles not in adapted material. Such resources should not be overlooked.

Methodology for the formation of a population for use as a source of varieties or hybrids has been described by Pandey et al. (1984). Individual materials can be planted as female rows and detasseled in an evaluation-cum-HS crossing block where the pollinator is an adapted local variety or a balanced mixture of all the materials. A minimum of 50 plants of each germplasm should be planted in 2-4 row plots 5 m long and detasseled. Throughout the growing season, notes should be taken on various characteristics of the materials. Inferior entries should be rejected and each selected entry should be bulk-harvested.

Evaluation of these testcrosses in 3-4 environments in replicated yield trials should provide reliable information on the GCA of the materials to be intermated to form the population. Two-row plots 5 m long and two replications at each location would generally be adequate to obtain reliable estimates of genotype and environmental effects. Multilocation evaluation of entries in a single season has been suggested to provide sufficient information for selection of superior entries (Comstock and Moll, 1963). The materials with acceptable GCA should be selected for intermating.

Thorough recombination among the materials must precede any improvement of the population. Recombination can be accomplished by planting the materials in a 2 or 3 females: 1 male arrangement, where individual components are the female and a balanced mixture (equal quantity of seed from each material mixed together) the male. In the first cycle, each entry can be represented by up to 500 plants and detasseled. In each entry, 50-60 superior plants should be identified during the growing season and 20-30 ears from these plants selected at harvest. A large number of plants of each entry at this stage is desirable as it will permit more intense selection within the materials. When it is necessary to recombine among materials with different maturities, staggered plantings of male rows in time and space is suggested. Use of neutral environments has been advocated during recombination to overcome the photoperiod sensitivity of the accessions originating from varying latitudes.

Each selected ear should be planted ear-to-row next season and detasseled and a balanced mixture of all the selected ears is used as the pollinator. Within each entry, the inferior rows can be rejected and 2-3 ears selected at harvest from the superior rows so that each original entry is again represented by 20-30 ears in the population. Lower selection intensity in the recombination phase reduces the frequency of deleterious alleles in the population without causing significant genetic drift. The selection intensity can be manipulated so that the population is made-up of approximately 500 ears, each cycle of recombination. Two to three additional cycles of intermating of the population should provide sufficient genetic recombination among the materials constituting the population and the identity of the components would largely cease to exist.

If one wishes to compare expected genetic progress using different intrapopulation recurrent selection systems applied to a specific population, one must have estimates of additive and nonadditive genetic variances and between and within plot environmental variances. For estimation of expected correlated responses in specific traits when single-trait or index selection is used, additive genetic covariances between the specific trait and the selection criterion are essential. Knowledge about characteristics of many maize accessions held in germplasm banks has not been available in the past, but efforts to obtain such information are currently under way. Even so, there will continue to be a lack of information about the kind of gene effects operating and the magnitude of genetic variances controlling quantitative traits.

All of the recurrent selection systems have proven to be effective in maize improvement (Sprague and Eberhart, 1977; Gardner, 1978, 1986). The choice of which system and which populations to use must be made by each breeder and will depend upon: 1) the ultimate goal--

variety or hybrid, 2) traits to be improved--yield, disease resistance, drought tolerance, etc. 3) time constraints--short term vs. long term, 4) germplasms available--locally adapted varieties, improved populations, pools and bank accessions, 5) knowledge about those germplasms, and 6) financial resources available.

If the ultimate goal is to develop and release an improved variety, one of the intrapopulation methods should be used with a population constructed so as to contain as many of the most favorable alleles at each locus as is possible. If the ultimate goal is a hybrid of some kind, then one of the interpopulation reciprocal recurrent selection systems allows one to take advantage of all the genetic variability in two contrasting populations. When population improvement is integrated with a hybrid program, RRS and RFS provide new S_1 lines (units intermated) each cycle. These can be advanced to S_2 lines during the testing phase, and those related to the best interpopulation crosses can be further inbred and/or topcrossed and evaluated in hybrids. RFS produces heterotic pairs of lines which may form a useful hybrid.

In early cycles of reciprocal selection involving two contrasting heterotic populations, intrapopulation selection in each has been as effective as reciprocal interpopulation selection in improving the interpopulation cross. In addition, intrapopulation selection has been more effective in improving the populations and derived inbreds (Odhiambo and Compton, 1989). This is not surprising since reciprocal selection in early cycles is likely to be more for GCA or additive effects, whereas, in the long run, additive genetic variance will be reduced and SCA involving dominance and epistasis effects will play a larger role in the interpopulation cross and in crosses between lines extracted from the improved populations. Recent evidence of Compton and Tragesser (Tragesser, 1991) indicates that improvement in the interpopulation crosses from intra- vs. interpopulation selection do differ in the kind of gene effects operating.

If the trait to be improved is controlled primarily by additive genetic effects and heritability is high, any intrapopulation system will be effective, including mass selection. S_1 family evaluation and selection has been particularly effective in the improvement of disease and insect tolerances, as well as many other traits. Selfing during population improvement improves inbreeding tolerance in the populations and reduces genetic load and time required for inbred and hybrid development (Odhiambo and Compton, 1989; Tragesser, 1991). If the trait is controlled by overdominance and by dominance types of epistasis and heritability is low, e.g. yield, then interpopulation systems are required to maximize yields.

If there is a need to produce a new variety or hybrid in a short time, elite populations with high mean yields but perhaps limited additive genetic variability should be used. If there are no time constraints, more exotic germplasm can be used to add more favorable alleles, favorable interacting alleles, and favorable interacting non-alleles and linkage groups to the population. To bring in new favorable alleles not available in adapted material, one frequently must introgress less well adapted germplasms, which brings in undesirable genes along with some good genes. Although one starts at a lower mean performance level, the greater additive genetic variability permits greater gains over a longer period of time to achieve a higher final level of performance in any variety released.

Financial resources available may dictate the choice of breeding system. Some systems require more hand pollination and skilled personnel. Replicated testing in multiple environments is expensive and requires trained personnel to properly conduct the experiments, collect the data, and analyze the results. Reciprocal selection programs require two populations and twice the work of intrapopulation selection. Costs must be weighed against potential benefits in making decisions about which breeding system to use.

VI. RECURRENT SELECTION METHODS USED IN THE TROPICS

A. SURVEY OF THE METHODS USED BY NATIONAL PROGRAMS

According to our survey of 48 maize scientists in Latin America, Asia, Africa, and the Middle East, HS, S_1, and FS family selection schemes were the most widely used breeding methods (approximately 50% of breeders used them) and received 17.9, 14.1, and 12.4% of the research resources, respectively (Table IV). MER selection (Lonnquist, 1964), MER selection$^+$ (CIMMYT, 1974), and MS were used by 38, 27, and 44% of the breeders sampled and used 9.3, 11.6, and 7.2% of their research resources, respectively. All breeders practiced population improvement and this activity used 60.6% of their research resources. Hybrid development (line development, evaluation of line combinations, etc.) was practiced by 85% of the breeders and used 39.3% of their research resources.

Table IV.

Population improvement methods used (%) and breeders (%) using them for the improvement of tropical maize. Results based on survey of 48 breeders of tropical maize from Asia, Africa, the Middle East, and Latin America.

Selection Methods	Resources	Breeders
	%	
1. Half-sib family	17.9	52
2. S_1 selection	14.1	54
3. Full-sib	12.4	46
4. Modified ear-to-row (Lonnquist, 1964)	9.3	38
5. Modified ear-to-row (CIMMYT, 1974)[a]	11.6	27
6. Simple mass selection	7.2	44
7. Selection for SCA	4.3	31
8. Selection for GCA	4.3	31
9. Stratified mass selection	5.6	25
10. Others	1.7	8
Population Improvement	60.6	100
Hybrid development	39.3	85

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[a] Described on pages 95-97.

Considerations of resource availability (27.3%), compatibility with program objectives (23.4%), and gains/resource use (20.1%) were major determinants of the method of selection breeders would use. Ease in implementation (11.0%) and stage of development of the germplasm being improved (9.1%) also affected choice of the breeding methods by the breeders. Other factors such as stage of development of the program and personal biases played relatively less important roles. Lack of financial and logistical resources, gains/resource used, and ease in implementation were cited as primary reasons for the use of HS, MS, and various MER selection schemes. Greater effectiveness at increasing frequency of desirable alleles and reducing the undesirable alleles and compatibility with hybrid development activities were cited as primary reasons for use of S_1 selection. Compatibility with program objectives and seed availability for multi-location testing were cited as primary reasons for use of FS selection.

Half-sib, S_1, and FS selection schemes were the most widely used methods across the four continents. Half-sib selection was the most important method in Asia and second most important method in the other three continents. Full-sib selection was the most important method in Latin America, third most important method in

Africa and the Middle East, and fifth in importance in Asia. S_1 selection was important in all continents except the Middle East. Only Latin America and Asia reported appreciable use of interpopulation selection schemes.

Population improvement was practiced by most of the scientists in the four continents and used 67.5% of the resources in Latin America, 54.7% in Asia, 52.5% in the Middle East, and 52% in Africa. Resources devoted to and scientists involved in hybrid development were 47.5 and 100% in the Middle East, 45.3 and 93% in Asia, 48 and 80% in Africa, and 25.7 and 79% in Latin America, respectively.

B. PROGRESS FROM SELECTION IN NATIONAL PROGRAMS

1. Mass Selection:

From the published reports, MS seems to have been used most commonly. Using this procedure, Johnson (1963) reported a yield gain of 11% per cycle in 'Tuxpeno' and Vencovsky et al. (1970) reported a gain of 3.8% per cycle after five cycles of selection in 'Paulista Dent' and 1.7% per cycle in 'Cateto M. Gerais' after three cycles of selection. Torregroza (1973) reported an increase of 48% in prolificacy and 35% in yield after 11 cycles of MS for increased prolificacy. Selection for single ear plants for 11 cycles decreased prolificacy by 16% and yield by 7% in the same population. Nine cycles of MS for prolificacy in the populations 'MB-51' and 'MB-56' increased prolificacy by 2.0% and 3.38% and yield by 3.0% and 5.45% per cycle in the two populations, respectively (Torregroza et al., 1976).

Arboleda-Rivera and Compton (1974) practiced MS for yield and prolificacy in a broad based Colombian composite. Selection was practiced during dry season (A), rainy season (B), and during both dry and rainy seasons (AB). Selection in the B season increased yield and prolificacy by 10.5% and 8.8% per cycle, respectively, in the B season and 0.8% and 1% in the A season. Selection in the A season improved yield and prolificacy by 2.5% and 4.4% per cycle in the A season and by 7.6% and 11.4% in the B season, respectively. Selection in both seasons improved yield and prolificacy by 5.3% and 7.0% per cycle in the B season and by 1.1 and 3.3% per cycle in the A season. Vargas-Sanchez (1990) evaluated gains from selection and genetic variances in the same population after 10 cycles of selection in the A season, 10 cycles in the B season, and 20 cycles in A and B seasons, using Design I. Selection in season A produced higher gains than in B but highest gains were obtained with selection in both seasons. Gains from selection for A, B, and AB seasons for prolificacy were 2.3, 2.0, and 3.8% and for yield 3.8, 3.4, and 5.3%, respectively. The additive genetic variance for prolificacy increased in each of the selected populations. For yield the additive genetic variance was greater in AB than in the other two versions. Selection in A season reduced additive genetic x environmental effects for yield, whereas selection in the B season increased those effects.

Genter (1976) practiced 10 cycles of MS in a composite of Mexican races and obtained a gain of 19.1% per cycle in yield. He also reported that the advanced cycles of selection had lower plant and ear heights, reduced moisture, days to silk, and smut infected plants, and improved synchronization of pollen-shed and silking. Darrah (1986) reported yield gains of 2.3% per year in 'Kitale Composite A' (KCA), after 10 cycles of selection.

Delgado and Marquez (1984) used MS to improve adaptation of the maize variety Zacatecas 58. In one scheme, selection was practiced separately at each of three sites and the selections were recombined at one site (convergent-divergent MS). In another scheme, one cycle of selection was completed at each of the three sites; only one site was involved in any given cycle (rotative MS). The results indicated that rotative MS was superior to convergent-divergent selection for improving adaptation of the population.

2. Half-sib Family Selection:

Paterniani (1967) reported gains of 13.6% per cycle in the yield of population Paulista Dent after three cycles of MER selection. After six years of MER selection, Darrah et al. (1978) reported gains of 0.83, 2.59, and -0.43% per year in the yields of 'KII', 'Ec573', and 'H611', respectively. After ten years of selection, they reported gains of 5.2% in the population KCA. Lima et al. (1974) obtained gains per cycle of 3% in 'Flint Composite' and 2% in 'Dent Composite' after two cycles of selection. After eight cycles of MER selection, Sevilla (1975) reported yield improvements of 9.5% per cycle in 'PMC-561'. Segovia (1976) obtained 3.2% per cycle gains in the initial three cycles and no gains in the later three cycles of ER selection in 'Centralmex'.

Gains per cycle from selection among and within HS families for yield have been reported to be 3.80% in the population 'Piramex' (Paterniani, 1968), 10.8% in Tuxpeno (Lima and Paterniani, 1977), 1.90% in 'IAC-1' (Miranda et al., 1977), 2.84% in 'IAC-Maya' (Sawazaki, 1979), 2.70% in 'Dentado Composto Nordeste' (Santos and Naspolini, 1986a), and 5.10% in 'Flint Composto Nordeste' (Santos and Naspolini, 1986b).

Eberhart and Harrison (1973) reported results of two cycles of selection in the population 'Kitale', where the S_1 lines were topcrossed to the parental population (tester). They obtained a 15% increase in yield after the two cycles of selection. The selected population yielded higher than the original population in both poorer and in better environments.

Santos and Naspolini (1986b) practiced three cycles of selection in the population Dentado Composto Nordeste and reported that additive genetic variance for ear weight decreased from C0 to C1 and then remained constant up to C3. Santos et al. (1988) reported 15.20% and 5.20% yield improvement per cycle in the populations Dent Composite and Flint Composite, respectively, after two cycles of MER selection. Darrah (1986) employed MER selection to improve KCA. Gains per year for yield after 10 cycles of selection were 2.9%, with no change in the performance of the population cross when crossed to its heterotic counterpart.

3. Full-sib Family Selection:

Jinahyon and Moore (1973) reported results of four cycles of selection. Yield increased by 7.9% per cycle and plant and ear heights and lodging decreased in their experiments. Darrah (1986) practiced FS selection to improve KCA. Gains per year after five cycles of selection were 3.6% for yield. Four cycles of FS selection for prolificacy were conducted by Singh _et_ _al_. (1986) in one variety. Linear response per cycle for prolificacy was greater under low plant density (5.5%) compared with that under high density (3.6%). They also reported a significant correlated response of 4.5% per cycle for yield and concluded that selection for prolificacy may be useful in developing high yielding, early, and short maize genotypes.

4. S_1 Family Selection:

Jinahyon and Moore (1973) reported a yield increase of 8.3% per cycle in 'Thai DMR Composite' after two cycles of S_1 selection. The selected population had 17% stalk lodging compared to 53% in C0. In 'Thai Composite-

1′ (later called Suwan-1), improvement in yield and downy mildew resistance were measured after nine and seven cycles of selection, respectively. Yields improved by about 5% per cycle and infection to downy mildew was reduced from 80% in C0 to less than 5% in C7 (S. Sriwatanapongse, 1990, personal communication). Darrah (1986) employed S_1 recurrent selection to improve KCA. Gains per year after five cycles of selection were 0.9%, with no change in the population cross when the population was crossed to its heterotic counterpart.

Gomez (1990) reported gains of 6.7**% per cycle in yield after two cycles, using a modification of S_1 selection scheme, where top ears of the plants were allowed to be open-pollinated and the second ears were selfed. The selfed ears were selected from higher yielding plants and planted next season ear-to-row as females and detasseled. A bulk mixture of all selfed ears served as the pollinator. Open-pollinated ears from the superior plants in visually selected S_1 families in the recombination block were used to initiate the next cycle.

5. Recurrent Selection Methods Used for Interpopulation Cross Improvement:

Vencovsky et al. (1970) practiced five cycles of SMS in Paulista Dent and three cycles in Cateto Minas Gerais. While heterosis between the two populations increased in the first cycle of selection, it decreased in the third cycle. The cross involving the third cycle of selection of Paulista Dent and first cycle of Cateto Minas Gerais exhibited maximum heterosis and the highest yielding cross involved fifth cycle of Paulista Dent and third cycle of Cateto Minas Gerais without significant heterosis.

Torregroza et al. (1972) practiced two cycles of RRS in the populations 'Harinoso Mosquera' and 'Rocamex V7' and reported increases of 4.5 and 15% per cycle in the yields of the two populations, respectively. The C1XC1 and C2XC2 yielded 32 and 34% higher than C0xC0. Gevers (1974) practiced three cycles of RRS and reported gains of 7.1, -0.5, and 3.3% per cycle in 'Teko Yellow', 'Natal Yellow Horsetooth', and the population cross, respectively, when the male parents were selected for agronomic traits. When random male parents were used, the yield improvements were 7.5, 7.4, and 5.8%, respectively. Darrah et al. (1978) practiced three cycles of RRS in the populations KII and Ec573 and reported gains of 4.96% per cycle in Ec573 and no gains in KII. The population cross showed an increase of 7.07% per cycle.

Paterniani and Vencovsky (1978) reported yield increases of 3.5% per cycle in the cross of the populations Dent Composite and Flint Composite after two cycles of RHS selection using prolific plants. Paterniani and Vencovsky (1977) also reported 7.5% gain in the population cross of 'Cateto' and Piramex using RRS. They attributed 4.3% of the gain to improvement of the two populations and 3.2% to change in heterosis of the population cross. Darrah (1986) compared three methods (MER, S_1, and RRS) for the improvement of the cross KSII x Ec573. Only Ec573 showed a response per year of 4.6% for MER and 3.5% for S_1 selection. Neither population responded to RRS. While 10 cycles of MER and S_1 selection did not improve the population cross, five cycles of RRS improved the population cross by 2.8% per year. Ochieng and Kamidi (1991) evaluated progress from eight cycles of RRS in the same two populations at several sites over three years. While no improvement was observed in either population, the varietal cross improved by 3.56% per cycle. Percent mid-parent heterosis increased significantly (b=3.80). Prolificacy increased in both the populations and in the population cross. Although maturity did not change in either parent, the variety cross was earlier. Ear height was reduced in Ec573 but did not change in KSII.

C. HYBRID DEVELOPMENT IN NATIONAL PROGRAMS

Generally, OPVs occupy 61% of the maize area and hybrids 39% in developing countries (CIMMYT, 1990). Exclusion of Argentina, Brazil, and China, the largest hybrid producers among the developing countries, increases percentage of area planted to OPVs to 84 and reduces percentage of area planted to hybrids to 16 (CIMMYT, 1987). The reasons for lower use of hybrids in the developing countries are insufficient yield advantage of hybrids under high stress and low yield conditions, limited financial resources for purchase of farm inputs, and lack of effective seed production and distribution systems (Paliwal and Sprague, 1981; CIMMYT, 1987). Nevertheless, when properly implemented, hybrid maize methodology has given good results in most tropical countries, particularly where a strong private seed industry is present (Paterniani, 1990).

One of the first hybrid development programs in the tropics was started in 1932 at the Agronomic Institute of

Campinas, Brazil, where selfing was done in a local orange flint cultivar, Cateto, to develop a flint hybrid (Paterniani, 1990). The first superior semi-dent hybrid was developed by crossing Cateto with a local yellow dent cultivar, 'Amarelao', at the School of Agriculture at Vicosa, Brazil. In a study involving 418 single crosses among 31 lines from Brazil, Colombia, and Mexico, Paterniani (1964) reported 55% superiority of yields in Colombian X Mexican lines over the best available double cross hybrid in Brazil. He also reported greater increase in yield, standability, disease resistance, and vigor in hybrids of improved materials compared to the original cultivars, Cateto and Paulista Dent. The first successful double cross hybrid developed in Brazil involved lines from Cateto and 'Tuxpan' (based on a cross between Tuxpeno from Mexico and a yellow dent from Georgia). Most of the current maize hybrid development in Brazil is based on Tuxpeno and Caribbean Flints (R. Magnavaca, 1991, personal communication).

In Venezuela, heterosis between ETO and some other Caribbean flints with Tuxpeno is exploited (Paterniani, 1985). In Colombia, hybrids mainly based on Caribbean germplasm have been developed; lately some Tuxpeno materials have also been used. In Peru, 'Perla' from Peru and flints from Cuba and Central America have been used for hybrid and composite development. Lately, Tuxpeno has played a more important role in hybrid development in Brazil due mainly to its heterotic potential with Cateto.

In a study involving 12 races of maize --4 dents, 5 flints, and 3 floury types, Paterniani and Lonnquist (1963) reported that F_1 crosses within endosperm type were as productive as between endosperm types. Castellanos et al. (1987) studied the use of S_3 lines in hybrid production in Guatemala. In one experiment, diallel crosses among 8 yellow S_3 lines and in another experiment diallel crosses among 10 white S_3 lines were evaluated at four locations. Up to 242% and 277% high-parent heterosis was detected in the two experiments, respectively. Superior lines had high GCA and their seed production potential was considered sufficient for their commercial use. This indicated that enough genetic variability exists within endosperm types and that not all hybrids need be between endosperm types.

Cordova (1984) reported on the performance and use of family hybrids developed in Guatemala during 1977-83 (Table V). Methodologies for development of hybrids using FS families were elaborated, as such families were more productive as seed parents and were relatively easier to maintain in successive seed increases. He reported high-parent heterosis of up to 54% among families derived from 'La Posta', 'Mezcla Tropical Blanca', 'Tuxpeno-1', and 'Tuxpeno Caribe'. On the basis of trials conducted at 33 locations during 1982, HB-83 was released in 1983. The superiority of HB-83 during 1982 averaged 37% over the local check. By 1984, approximately 2,500 tons of seed of all nonconventional hybrids were produced which reduced maize seed importation by 90%. Such nonconventional hybrids are superior in their yield and stability to many of the commercial hybrids as well (Cordova, 1990; Azofeira and Jimenez, 1988; Perez _et al._, 1988).

Table V.

means across locations? years?

Yield of white seeded maize varieties and hybrids evaluated at 183 locations in Guatemala during 1978-81.

Material	Yield
	t/ha
HB-33	4.43
HB-19	4.34
ICTA T-101	4.33
H-5 (Commercial Check)	4.21
HB-67	4.21
HB-69	4.03
La Maquina	3.98
ICTA B-1	3.81
CRIOLLO (Check)	3.33

Search for heterosis between introduced germplasm and local maize strains was initiated in 1959 in Kenya. Crosses of KSII with Ecuador 573 and Costa Rica 76 yielded 40% more than the best parent, KSII. Based on this information a varietal cross H611, (KSII x Ecuador 573) was released in 1964. A double cross, H622, and a three-way hybrid 632 were released for commercial production in 1965. Other hybrids released to date include H612, H613, H614, and H625. Hybrid maize in Kenya has become so popular that most farmers in high- and medium-yield potential areas will not grow OPVs. However, OPVs yielding 4-24% higher than the commercial hybrid H-625 have recently been identified (Ochieng, 1986; Mwenda, 1986). The maize breeding program of Zimbabwe is totally oriented toward hybrid development. Twenty-eight composites have been developed based on their heterotic patterns. Since 1932, 14 double cross hybrids, four three-way hybrids, six single crosses, and four modified single crosses have been developed. The seed production and promotion of the hybrids is efficiently carried out by the Seed Association of Zimbabwe (Oliver, 1986).

Singh (1986) reported that hybrids based on local flint germplasms were inferior to those developed from local x exotic (USA) or flint x dent crosses in India. Based on local x USA or Central American materials, four double cross hybrids were identified in 1961. By 1985, 18 double cross or double topcross hybrids of medium to full-season maturity had been released to the farmers.

Kim _et_ _al_. (1990) conducted a diallel trial involving five tropical and five tropical x temperate maize lines to determine their combining ability. The GCA effects accounted for approximately 80% of the total genetic variance. In Nigeria, the five tropical inbreds showed positive GCA effects in forest region and three tropical and two nontropical inbreds showed positive GCA effects in the savanna. The GCA effects were more important in crosses among tropical lines and the SCA effects were more important in crosses involving tropical and nontropical lines.

D. RECURRENT SELECTION AT CIMMYT

The activities of the various units in CIMMYT's maize program and their experiences and information are briefly summarized here. The results reported apply largely to selection methods used and progress made prior to 1985. Data on the effectiveness of the new methodologies will be available in the near future. A list of CIMMYT's maize pools and populations developed and improved for tropical lowlands is presented in Table VI. A more comprehensive list and description of materials and the germplasm involved in their formation is given by CIMMYT (1982).

Table VI.

Maize gene pools and populations developed and improved by CIMMYT for tropical lowlands.

Names of materials	Other name′
Gene pools:	
Tropical Early White Flint (TEWF)	Pool 15
Tropical Early White Dent (TEWD)	Pool 16
Tropical Early Yellow Flint (TEYF)	Pool 17
Tropical Early Yellow Dent (TEYD)	Pool 18
Tropical Intermediate White Flint (TIWF)	Pool 19
Tropical Intermediate White Dent (TIWD)	Pool 20
Tropical Intermediate Yellow Flint (TIYF)	Pool 21
Tropical Intermediate Yellow Dent (TIYD)	Pool 22
Tropical Late White Flint (TLWF)	Pool 23
Tropical Late White Dent (TLWD)	Pool 24
Tropical Late Yellow Flint (TLYF)	Pool 25
Tropical Late Yellow Dent (TLYD)	Pool 26
Tropical White Flint QPM	
Tropical White Dent QPM	
Tropical Yellow Flint QPM	
Tropical Yellow Dent QPM	

Table VI. Continued.....

Maize populations:

Tuxpeno-1	Population 21
Mezcla Tropical Blanco	Population 22
lanco Cristalino-1	Population 23
Antigua-Veracruz 181	Population 24
Blanco Cristalino-3	Population 25
Mezcla Amarilla	Population 26
Amarillo Cristalino-1	Population 27
Amarillo Dentado	Population 28
Tuxpeno Caribe	Population 29
Blanco Cristalino-2	Population 30
Amarillo Cristalino-2	Population 31
ETO Blanco	Population 32
Antigua-Republica Dominicana	Population 35
Cogollero	Population 36
Tuxpeno o_2	Population 37
Yellow QPM	Population 39
White QPM	Population 40
Composite K o_2	Population 41
La Posta	Population 43

Table VI. Continued.....

Early Yellow FlintQPM	Population 61
White Flint QPM	Population 62
Blanco Dentado-1 QPM	Population 63
Blanco Dentado-2 QPM	Population 64
Yellow Flint QPM	Population 65
Yellow Dent QPM	Population 66

1. Back-up Unit (Germplasm Development Unit):

The Back-up unit, more recently named Germplasm Development Unit, develops and improves germplasm with a broad genetic base that can either be used as new populations for international testing or for providing superior families for introgression into the existing populations. Several gene pools for different climatic conditions and with different maturity, grain color and texture have been developed over the years. The methodology involved in their development and improvement has been described by Vasal *et al*. (1982), Pandey *et al*. (1984), and De Leon and Pandey (1989).

Pools were improved by means of MER selection of Lonnquist (1964) with some alterations. In each cycle of selection, approximately 500 HS families making up a gene pool were planted in isolation in an arrangement of two females to one male. Each ear selected in the previous cycle was planted in an individual female row. Male rows were planted with seed prepared by mixing approximately 60 seeds of only those ears that came from superior families in the previous cycle. For each family, generally only one replication was grown in a 5 m row that included 16 to 21 plants. All female rows and undesirable male plants were detasseled prior to pollen shedding. For selection of families, data on yield, plant and ear height, days to silking, lodging, disease and insect reaction, and plant and ear uniformity were recorded at appropriate stages of plant development. The male rows closest to a female row served as a check in the selection. From the superior families identified (about half of the total), one to three ears were selected from good plants and planted as new families in the next cycle of selection. One cycle of selection was completed in a season. New germplasm was added to the gene pools regularly, as described previously. Pools were also improved for specific diseases and insects under artificial inoculations and infestations. The choice of stresses to be imposed in the selection process in a given pool was based on its susceptibility and on the importance of those stresses in the area of the world where the pool would be useful.

In a comparison of cycles of selection for eight tropical pools conducted at two sites, progress (linear response) averaged 2.50 (significant at the 0.01 probability level), -0.15, -0.35, -1.66, and -0.90% per cycle for yield, days to silking, plant height, stalk-rot score, and % ear-rot, respectively (De Leon and Pandey, 1989). Yield improvement was greater in pools selected for stalk-rot resistance (3.02% per cycle) than in those selected for ear-rot resistance (1.38% per cycle). In the reduction of days to silk and plant height, however, greater progress was made in pools selected for ear-rot resistance (-0.50 and -0.75% per cycle, respectively) than in those selected for stalk-rot resistance (-0.04 and -0.25% per cycle, respectively). Results indicated that the selection scheme was effective in increasing grain yield and ear- and stalk-rot resistance and reducing days to silking and plant height (Table VII).

Table VII.

Means for different cycles of selection in eight tropical gene pools evaluated in two tropical environments.

Pool	Cycle	Yield	Days to silking	Plant ht	Stalk rot rating	Ear rot
		t/ha	no.	cm	1-5[a]	%
TEWF	CO	3.62	65	172	3.9	--
	C5	4.40	66	158	3.7	--
	C8	4.36	64	158	3.3	--
	C11	4.33	62	155	3.2	--
LSD (0.05)		0.57	1.4	7.9	0.2	--
TEWD	CO	3.48	65	171	3.8	--
	C5	4.52	65	161	3.5	--
	C8	4.84	65	162	3.1	--
	C11	5.14	63	162	3.1	--
LSD (0.05)		0.38	0.8	9.0	0.2	--
TEYF	CO	2.69	65	152	4.1	--
	C5	3.73	66	157	3.9	--
	C8	3.93	64	148	3.6	--
	C11	4.36	62	151	3.3	--
LSD (0.05)		0.44	1.6	4.8	0.3	--

Table VII. Continued.....

TEYD	C0	2.72	65	146	3.8	--
	C5	4.42	66	149	3.4	--
	C8	4.12	65	147	3.2	--
	C11	4.62	62	148	2.9	--
LSD (0.05)		0.35	1.0	8.5	0.3	--
TIYD	C0	5.46	72	199	3.5	--
	C7	5.89	69	175	3.2	--
	C12	5.83	71	177	3.1	--
	C16	6.40	70	182	2.8	--
LSD (0.05)		0.63	2.2	6.6	0.2	--
TLWF	C0	5.98	73	201	3.4	--
	C7	5.55	71	182	3.4	--
	C11	5.92	70	169	2.9	--
	C15	6.18	70	171	2.7	--
LSD (0.05)		0.46	2.0	7.5	0.2	--
TIWD	C0	4.43	73	190	--	31
	C7	4.31	70	169	--	35
	C10	4.62	69	167	--	31
	C15	5.19	67	168	--	24
LSD (0.05)		0.37	2.1	4.3	--	--

Table VII. Continued.....

TLYF	C0	4.04	74	201	--	26
	C5	3.89	73	192	--	23
	C9	4.33	71	183	--	22
	C14	4.86	70	186	--	15
LSD (0.05)		0.44	1.0	13.4	--	--
Gains/ cycle (%)[b]		2.50	-0.15	-0.35	-1.66	-0.90

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[a] 1=good; 5=poor.

[b] All gains were significant at the 0.01 level of probability.

2. Advanced Unit:

CIMMYT maize populations that showed potential in preliminary evaluations in the cooperating countries and that had an acceptable level of phenotypic uniformity were further improved through international testing and selection of the superior FS families based on those tests. Because the main growing season in the northern hemisphere was from April to September and in the southern hemisphere from September to April, one cycle of selection was completed in four seasons (two years). The FS families were developed during October to April in Mexico. Data reported were based on evaluation of 250 FS families of each population along with six local checks at six lowland tropical locations. The progeny trials were grown in the northern hemisphere during April to September (Season 1). One of the trials from each population was usually grown in Mexico. A simple 16x16 lattice design was employed. Each plot consisted of 22 plants in a single row at a density of approximately 53,500 plants per ha. While the trials were grown in the southern hemisphere, the 250 FS families were planted in 10-m rows in the breeding nursery in Mexico (Season 2). Approximately 50% of the desirable plants of each family were selfed. For selfing, plants were selected for one or more of the following major traits: shorter plant height, earlier maturity, resistance to SCB, resistance to FAW, resistance to ear rot, and resistance to stalk rot. Selections for insect and disease resistance were practiced under artificial infestation and inoculation (Vasal et al., 1982; Pandey et al., 1986).

At harvest, two to three S_1 ears were selected from each FS family. Each S_1 ear was identified by its parental FS family and planted ear-to-row in Mexico in a 16-plant plot the next season (Season 3). Based on the international progeny test data across locations, about 100 FS families were selected. Better S_1 families from the selected FS families were identified, and approximately 50% of the plants within them selected and pollinated with a mixture of pollen from selected plants of most of the selected S1 families. Selection was again practiced for the major trait. At harvest, two to three HS ears were selected from each selected FS family. Sixty-four plants of each HS ear were grown ear-to-row in Mexico in the next season (Season 4). Superior HS families in each FS family were identified and reciprocal plant-to-plant crosses made between them ensuring that the two HS families involved in a cross came from different FS families. It should be noted that the FS families were selected on the basis of international progeny test data, and selection for the major trait was emphasized during the selfing and bulk sibbing generations.

Introgression of germplasm from the backup pools was made regularly into the populations. When the progeny trials were growing in the southern hemisphere, approximately 50 HS families of the appropriate backup pool were planted alongside the FS families of the population in a nursery in Mexico. During this and subsequent seasons, pool families were handled exactly like population families, but no crosses were made between population families and the pool families. At harvest, about 220 FS pairs from the population and 30 FS pairs from the backup pool were selected to make up the 250 FS families for the international trials. The backup pool families equal to or superior in performance to the mean of the population were used along with families selected from the population for the next cycle of selection.

Results of progress made in four medium maturity populations for some important agronomic traits are presented in Table VIII. Gains per cycle averaged over the four populations in seven environments for yield, days to silk, ear height, and ears per plant were 2.11 (significant at the 0.01 probability level), -0.31, -0.47,and 1.05%, respectively (Pandey et al., 1987).

Table VIII.

Performance of different cycles of selection of four medium maturity tropical maize populations grown in seven environments in 1983-84.

Populations	Cycles	Yield	Days to silk	Ear ht	Ears/ plant
		t/ha	no.	cm	no.
Blanco Crist.-1	C0	5.11	64	113	0.91
	C2	5.64	62	103	0.98
	C5	5.29	63	108	0.97
Mezcla Amarilla	C0	4.97	63	108	0.96
	C2	4.64	62	93	0.96
	C5	5.40	60	101	0.98
ETO Blanco	C0	4.84	64	108	0.88
	C1	5.04	65	111	0.92
	C4	5.46	64	104	0.96

Table VIII continued.....

Ant. Rep. Dominic.	C0	4.66	59	94	0.95
	C1	4.53	59	87	0.92
	C4	5.13	59	92	0.98
LSD ($P<0.05$) within popul.		0.28	0.7	5	0.04
Gains per cycle (%)[a]		2.11	-0.31	0.47	1.05

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[a] All gains are significant at the 0.01 level of probability.

Another trial was conducted in six environments involving different cycles of selection of eight late maturing tropical populations (Pandey et al., 1986). Gains per cycle for yield, days to silk, ear height, and ears/plant averaged 1.31, -0.59, -1.77, and 0.87% across the populations and locations (Table IX).

Table IX.

Performance of different cycles of selection of eight full-season tropical maize populations grown in six environments in 1983-84.

Populations	Cycles	Yield	Days to silk	Ear ht	Ears/ plant
		t/ha	no.	cm	no.
Tuxpeno-1	C0	5.98	66	112	0.96
	C2	6.04	65	110	0.97
	C5	6.34	66	114	0.96
Mez. Trop. Blanca	C0	6.09	68	127	0.94
	C2	6.50	66	124	0.95
	C4	6.55	65	119	0.97
Ant. Veracruz-181	C0	5.68	67	127	0.96
	C2	5.33	67	117	0.94
	C5	5.76	66	117	0.96

Table IX. Continued.....

Amarillo Crist.-1	CO	5.27	68	120	0.94
	C2	5.28	67	123	0.95
	C5	5.75	66	117	1.00
Amarillo Dentado	CO	6.02	68	133	0.99
	C2	6.03	66	126	0.96
	C4	6.39	65	115	1.04
Tuxpeno Caribe	CO	6.20	67	120	0.93
	C2	6.01	66	122	0.92
	C5	6.21	65	111	0.95
Cogollero	CO	5.71	66	136	0.93
	C2	5.57	66	131	0.98
	C5	6.25	63	114	0.99
La Posta	CO	6.12	70	146	0.91
	C2	6.26	69	142	0.96
	C4	6.58	67	130	0.98
LSD ($P<0.05$) within Popul.		0.31	0.8	5	0.04
Gains per cycle (%)*		1.31	-0.59	-1.77	0.87

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* All gains are significant at the 0.01 level of the probability.

Villena (1974) practiced two cycles of FS selection in three maize populations, where evaluation of progenies was conducted in Central America and Mexico. The yield superiority of C2 over C0 was 33%, with a range of 29-36%. Paliwal and Sprague (1981) reported gains per cycle for yield ranged between 0.8 and 9.8% in 13 maize populations with an average of 3.4%. The gains depended on relative yield and genetic variability of the populations.

3. Development of Experimental Varieties (EVs) and their performance:

On the basis of data of progeny trials at each site, approximately 10 FS families were selected and intermated (plant-to-plant crosses among families) using remnant seed to form an EV. The name of the EV was derived from the name of the site where the progeny test was conducted, followed by two digits indicating year of test. The last two digits indicated the population number. Thus, the EV 'Poza Rica 8121' was developed by intermating 10 FS families of the population 'Tuxpeno-1' (Population 21) whose 250 FS families were evaluated at Poza Rica, Mexico, during 1981. Data from all sites where a population was tested were used to select 10 FS families for the formation of the 'across experimental variety', e.g., 'Across 8121'. At harvest, clean ears from each family resulting from crosses with other families were saved and shelled in bulk. An equal quantity of seed was taken from each family bulk and mixed together to make an F_1 bulk. The F_1 bulk was advanced to F_2 and the ears saved were shelled in bulk to provide seed for experimental variety trials (EVTs), elite variety trials (ELVTs) (best from the EVTs), and for distribution to CIMMYT's collaborators upon request. National programs grew EVTs and ELVTs, along with their own checks, to identify potentially superior maize germplasm for use in their programs.

Forty Poza Rica and Across EVs developed from C0 and C3/C4 of 10 populations were evaluated in four environments in Mexico to measure performance and stability. Poza Rica EVs were derived on the basis of Poza Rica summer data and the Across varieties were developed on the basis of data from 5-6 locations. Percent superiority of EVs derived from C3/C4 over those from C0 was 9.5 (significant at the 0.01 probability level) for yield, -2.6 for days to silk, -5.1 for plant height, -9.6 for ear height, 5.6 for prolificacy, and -11.7 for ear rating (Table X). Poza Rica EVs were lower ($P<0.01$) in plant and ear height (-6.1 and -10.3 %, respectively) than Across EVs during summer at Poza Rica and Across EVs had fewer (-1.19%) days to silk than Poza Rica EVs at the other three sites. The results indicate that EVs developed from advanced cycles of populations undergoing recurrent selection have greater yield (P<0.01) and are superior in other agronomic traits to those derived from original cycles (Pandey et al., 1991).

Table X.

Performance of Poza Rica and Across EVs derived from different cycles of selection of ten tropical maize populations. EVs were grown at four Mexican sites in 1983-84.

Type of Variety	Yield		Days to Silk	Plant Height
	t/ha	b[a]	no.	cm
Poza Rica EVs	4.92	1.05	76	189
Across EVs	5.09	0.95	76	193
LSD (P<0.05)	0.19	0.15	0.4	2.7
EVs CO	4.78	1.06	78	196
EVs C3/C4	5.23	0.94	76	186
LSD (P<0.05)	0.13	0.08	0.3	2.3

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[a] Stability parameter of Eberhart and Russell (1966).

4. Selection for Reduced Plant Height, Foliage, and Tassel Size:

A modified FS selection scheme was employed for reducing plant height in an extremely tall population Tuxpeno (Johnson et al., 1986). The criterion for family and plant selection was a visual assessment of the shorter genotypes at the time of pollination. Plant-to-plant crosses between selected families were made using approximately five plants per family, each plant being crossed with a plant in one of the other selected families. Two or three ears were saved from each selected family at harvest to retain about 300 families in each generation. Some families selected at the time of pollination were rejected at harvest for either their poor yield performance (visual) or reaction to diseases. Selection and recombination were achieved in the same season, allowing 2 cycles of improvement per year. This process was repeated from C1 to C12, at Poza Rica, Mexico, at an elevation of 60 masl and a latitude of 19° N. From C12 onward, families were visually evaluated in observation nurseries at Obregon (10 masl, 28° N latitude) in summer, and Tlaltizapan (900 masl, 19° N latitude) in winter, in addition to the location used for crossing (Poza Rica). The observation nurseries were planted one to two weeks in advance of the crossing block so that information on family height could be used in selection prior to pollination at Poza Rica. In the earlier generations, the plant population of the crossing block was 53,000 plants/ha. From C12 onward, the crossing block was grown at a higher population density of 106,000 plants/ha. Families with poor performance at higher density were eliminated. Pollinations were made among shorter plants with good synchronization of pollen shed and silking under density stress.

Cycles 0, 6, 9, 12, and 15 were evaluated at two or three locations in Mexico during 1978-79 to measure direct and correlated responses to selection. Selection was effective in reducing plant height from 282 to 179 cm (2.4% per cycle). The reduction in plant height was accompanied by 4.4% increase in yield (from 3.17 to 5.4 t/ha), 4.14% increase in kernel no./m^2 (from 1592 to 2667 kernel/m^2), and 3.1% increase (from 0.30 to 0.45) in harvest index per cycle, at the optimum plant density (Table XI). Optimum plant density for yield also increased by 2.1% per cycle (from 48,000 to 64,000 plants/ha). No change was noted in leaf area index, total dry matter production/m^2, effective filling period, or kernel weight at the optimum plant density (Johnson _et al_., 1986).

Much of the improvement in yield potential of the shorter plant selections during the initial six cycles was due to their ability to respond to higher plant populations without lodging, while maintaining or reducing the level of barrenness. Further increases in the density for optimum grain yield (density tolerance) was due to a reduction in the number of barren plants particularly for the cycles following C12 which were selected under a higher plant population. Reducing the number of barren plants was associated with a shortening in the interval between anthesis and silking.

If the relationship between grain yield and population density for the shorter plant selection is extrapolated to those densities (approximately 30-35,000 plants/ha) currently being achieved by farmers in the tropics, yield would be greater for the C0. The higher yield potential of the shorter varieties is only expressed at higher density. This improvement in tropical maize is similar to that which occurred between 1930 and 1970 in the USA Corn Belt. For farming conditions in the tropics in which weed management and crop nutrition are being improved, it is important to have a responsive and efficient genotype in order to maximize grain yield from those inputs. Selection for optimum plant height, yield, and density tolerance would provide management responsive and stable maize varieties for the farmers in the tropics (Johnson et al., 1986).

Table XI.

Plant height, lodging, grain yield, and harvest index for selections for reduced plant height in Tuxpeno grown at two to three locations during 1978 and 1979 in Mexico.

Cycle of selection	Plant height	Grain yield Plants/ha 64,000	 50,000	Lodging	Harvest index
	cm	t/ha	t/ha	%	
0	282	3.17	3.13	43	0.30
6	219	4.29	4.24	12	0.40
9	211	4.48	4.31	14	0.40
12	202	4.93	4.71	9	0.41
15	179	5.40	5.03	5	0.45
LSD (P.05)	22	0.30	0.37	7	0.04
Least squares change (%) per cycle[a]	-2.39	4.43	3.74	-	3.10

[a] All gains were significant at the 0.01 level of probability.

The large and almost linear response in plant height to selection indicates considerable additive variance for this trait. Even after fifteen generations of selection, there still existed considerable variation for the trait in the population. When the short plant selections are crossed with other materials, the F_1 is approximately intermediate in plant height (Cordova et al., 1979). The short plant selections are used intensively in national programs, where they are crossed with taller materials of other backgrounds in order to develop OPVs and hybrids with good plant stature, (Cordova et al., 1980).

There is evidence that careful removal of the male inflorescence prior to flowering increases grain yield (Poey et al., 1977). Most tropical maize cultivars have a large tassel that negatively affects yield and tends to be associated with higher ear placement (Paterniani, 1981). Also, yield per unit of leaf area is low for tropical materials. Reducing individual plant leaf area while maintaining or increasing grain yield per plant would increase the efficiency of grain production per unit leaf area. Subsequent increases in leaf area index through density management might further increase grain yield per unit area (Paterniani, 1990).

Fischer *et al*. (1987) reported results of six cycles of FS selection for reduced tassel branch number and for reduced leaf area density above the ear (LADAE) in the populations Tuxpeno-1 and Antigua-Republica Dominicana. Selection for each trait was practiced separately. In another population, ETO Blanco, simultaneous selection was practiced for both traits. Evaluation of C0 and C6 of single trait selections and C0, C2, C4, and C6 of combined trait selection was made at several densities at three sites in two years in Mexico. Gains per cycle for tassel branch number, LADAE, grain yield, and harvest index, respectively, were: (i) Tuxpeno-1: selection for reduced tassel branch number: -7.4*, not significant (NS), 2.2*, and 2.4*%; selection for reduced LADAE: -1.2*, -3.8*, NS, and 3.8*%; (ii) Antigua-Republica Dominicana: selection for reduced tassel branch number: -8.6*, -1.6*, 2.4*, and 2.2%*; selection for reduced LADAE: -5.7*, -2.6*, 2.0*, and 2.2%*; and (iii) ETO Blanco, selection for reduced tassel branch number and LADAE: -6.8, -1.8*, 2.5*, and 2.9*%, respectively. In all populations, selection increased yields of the genotypes under higher density and decreased anthesis to silking interval (ASI), and days to 50% silking. Increase in grain yield potential (yield at optimum density) was due to an increase in harvest index. The number of grains/leaf area increased in these selections, which represents an increase in grain sink (grain number) relative to source (leaf area surface). The proportion of dry mater produced after flowering that was stored as grain (partitioning index) did not change in these selections. The increased grain yield, brought about by selection for reduced plant height, foliage or tassel, suggests that a decrease in tassel branch number and leafiness would provide further improvement in the yield and stability of tropical maize (Fischer *et al*., 1987).

5. Selection for drought resistance:

Tropical maize often suffers significant yield losses due to drought which can occur any time during the crop cycle. A program was initiated during 1975 in Tuxpeno-1 (referred to as Tuxpeno Seleccion Sequia) to improve its drought tolerance (Fischer *et al*., 1983). Full-sib progenies of C1 of Tuxpeno-1 were grown at Tlaltizapan in the dry season. Selection criteria, developed on the basis of their relationship to yield among various varieties in previous trials, under irrigated and stress conditions were:

(a) relative leaf and stem elongation rate,
(b) Anthesis-to-silking interval,
(c) Leaf senescence score during grain filling,

(d) Canopy temperature from C3 onwards, and

(e) Yield.

Approximately 80 families were selected each cycle based on an index developed using the above traits. Fischer _et_ _al_. (1983, 1989) reported results of evaluations conducted on the first three cycles of selection both under stress and non-stress conditions. Yields increased by 9.5% per cycle under drought while little yield improvement occurred under non-stress conditions. Selection increased total dry matter under stress, root activity at 120-150 cm depth, ears per plant, and harvest index. Grain yield was correlated with ASI (-0.71*), relative leaf elongation (0.65*), and canopy temperature (-0.35*) under stress conditions and with leaf area index (-0.64*) under non-stress conditions.

Bolanos and Edmeades (1987) and Bolanos _et_ _al_. (1990) evaluated cycles 0, 2, 4, 6, and 8 of Tuxpeno Seleccion Sequia during the dry season of 1987-88 at Tlaltizapan. Cycle 8 yielded 0.80-0.90 t/ha more than C0 under environments with mean yields of 0.50 to 8.00 t/ha. Cycle 6 did not differ from C8, suggesting that perhaps genetic variability for the trait was reduced. The average gains at yield levels of 2 t/ha induced by drought stress at flowering were similar to those reported by Fischer et al. (1989). Selection increased ears per plant and harvest index by 1% per cycle without affecting total biomass, and reduced ASI. Number of grains and yield were reduced 10% for each day of delay in silking relative to anthesis, and after 10 days of delay the yield was practically zero. The latter cycles of selection had a greater accumulation of dry matter in the ear prior to flowering in all environments. The increase in dry matter in the ear increased by 18.2% under drought and 9% under optimum conditions. With an increase in the ear weight, there was a reduction in the tassel weight, perhaps because they competed for the same available photosynthates (Bolanos et al., (1990).

Byrne et al. (1989) compared cycles 0, 2, 4, 6, and 8 of Tuxpeno Seleccion Sequia with cycles 0, 2, 4, and 6 of Tuxpeno-1 improved through international testing, in 12 environments with varying levels of moisture. A 1.6% yield gain per cycle was obtained for the drought selected population vs. 1.2% per cycle for the same population improved through international testing.

Bolanos *et al*. (1990) concluded that:

1. There is sufficient genetic variability in CIMMYT maize germplasm for yield and ASI for improvement in drought tolerance. Stress should be manipulated to maximize expression of this variability.

2. Drought reduces number of grains and number of ears due mainly to silk delay and loss of silk viability.

3. The genetic variability for ASI under drought is due to differential capacity for accumulation of dry matter in the ear. Genotypes with reduced ASI are more drought tolerant.

4. Gains made for drought tolerance to date are largely due to better distribution of dry matter to the ear and selection for ASI under stress may increase yield potential in all environments.

6. Selection for Early Maturity:

Early maturing varieties offer flexibility in planting dates under rainfed conditions, opportunity for increasing cropping intensity, and the flexibility for escaping drought that may occur at the beginning or end of the growing season in the tropics. Early cultivars facilitate early land clearing and help conserve soil moisture for the next crop. Early cultivars permit an early harvest of the crop, when scarcity of food is common, as occurs among subsistence farmers in Africa, Asia, and Latin America.

Early maturity is generally associated with reduced yield. Therefore, in 1975, CIMMYT undertook a program aimed at developing earlier maize varieties without sacrificing grain yield in the tropical environments. Several approaches were tried:

1. Development of early populations by crossing low yielding early materials from the tropics and subsequent selection for higher yield while maintaining earliness. This approach was not successful as the recovery of yield potential proved difficult.

2. Introgression of different levels of temperate germplasm into tropical maize and subsequent selection for disease resistance, higher yield, and early maturity. This approach too was dropped after a few cycles of selection because of extreme disease

and insect susceptibilities of temperate maize in the tropical environment.

3. Development of populations by crossing early, lower-yielding tropical maize types with intermediate maturity and higher-yielding tropical materials and subsequent selection for early maturity and yield. This methodology was used in the development of early tropical gene pools. The pools were improved using the procedure described below and progress was made for early maturity, yield, and other traits (De Leon and Pandey,1989).

4. A population 'Compuesto Seleccion Precoz' was formed by recombining intermediate and early maturing families of late maize populations. A HS selection program was initiated in the population in 1976, and two cycles of selection were completed each year in two locations, Poza Rica and Tlaltizapan, Mexico, with a total of 15 cycles of selection.

The selection procedure involved in approaches 3 and 4 above involved planting of 500 HS families in a structure of 2 females:1 male. The male was the bulk of the superior families of the population. Each family was planted in a 5-m row with standard row spacing of 0.75 m and plant-to-plant spacing of 0.33 m. Thus a density of 43,600 plants/ha was maintained for the females and the density in male rows was 87,200. The higher density in the male rows was used to select for tolerance to density pressure by eliminating weak, lodged plants and plants with poor synchronization of anthesis and silking. These undesirable plants, together with plants in the female rows, were detasseled before anthesis. In the male rows, when 70% of the plants had silked, all plants were detasseled and, at anthesis, early plants in the female rows were marked. Final selection was made from these plants. At both locations, materials were harvested relatively early to aid in the visual separation of drier ears from the superior plants previously selected for earliness. These ears were used for initiating the next cycle.

Islam, Pandey, and Diallo (unpublished data) evaluated cycles 0, 4, 8, and 12 of Compuesto Seleccion Precoz in four tropical environments in Mexico at densities of 53,000, 80,000, and 106,000 plants per ha. A reduction of 0.5 day per cycle in days to 50% silking (69 days for C0 vs. 61 days for C12) with little reduction in grain yield (4.8 t/ha for C0 vs. 4.3 t/ha for C12) was observed.

Narro (1988) evaluated cycles 0, 3, 6, 9, 12, and 15 of Compuesto Seleccion Precoz at Ames (Iowa), Cali (Colombia), and Chiclayo (Peru) during 1987, at two densities of 53,000 and 75,000 plants/ha. The results indicate that the method employed was useful in reducing days to maturity, plant and ear height and leaf area and increasing prolificacy (Table XII). The changes in yield, averaged over the three locations, varied with cycles and were nonsignificant. The yields increased at Ames, decreased at Chiclayo, and remained the same at Cali, with increasing cycles of selection. The changes in the traits were linearly related to cycles of selection. The later cycles yielded particularly better at Ames, due mainly to shorter growing cycle. No cycle x density interaction was observed. Narro (1988) concluded that development of early maturing and high yielding cultivars for a given site would be more effective, if practiced at that site.

Table XII.

Progress from selection for early maturity and other traits in the population Compuesto Seleccion Precoz at three locations (Ames, Iowa; Cali, Colombia; and Chiclayo, Peru) during 1987.

Cycles of selection	**Yield**	**Days to 50% silking**	**Plant height**	**Ear height**	**Leaf area**	**Ears/ plant**
	t/ha	no.	------cm------		cm^2/plt	no.
0	3.2	71	209	112	6300	0.74
3	2.8	67	193	96	5816	0.73
6	3.4	65	192	94	5738	0.79
9	3.1	64	188	91	5530	0.77
12	3.4	60	176	82	5340	0.81
15	3.2	58	172	75	5097	0.81
LSD 0.05	0.40	2.3	5.6	3.3	219	.0.05
Gain/cycle[a]	ns	-1.0	-1.2	-2.0	-1.3	0.72

[a] Gains for all traits, except yield, were significant at the 0.01 level of probability.

7. Selection for Nitrogen Use Efficiency:

Maize yields vary with the supply of N and N is frequently deficient in tropical soils, where supply of chemical fertilizers is also limited (Edmeades and

Lafitte, 1987). Most breeding programs develop cultivars under high input levels under the assumption that a variety superior under such conditions would also be superior under low input levels, though by a reduced margin. In 1985, CIMMYT initiated a study to show whether it was possible to select for improved performance of maize under N stress without sacrificing its responsiveness to high N levels. Preliminary results obtained by evaluating 18 entries (16 improved materials and 2 landraces; 12 late and 6 early maturing) indicated that there was no correlation between grain yield and chlorophyll concentration at flowering and grain filling at high N level. Yield and chlorophyll content in the ear leaf, two weeks after silking, however, were closely correlated under low N level. The entries x N interaction was significant at the 8% level of probability, indicating that selection under N stress might be justified. Two hundred fifty FS progenies of a variety, 'Across 8328', were evaluated both under 0 and 200 kg N/ha levels in 5-m row plots. A 20% selection intensity was applied and selection was based on an index that comprised grain yield under N stress and without N stress, and high ear-leaf chlorophyll content during grain filling, short ASI, and large leaf area under N stress. During the first cycle of selection, families that yielded well under limited N also retained their lower leaves in a functional state for a longer time and had a shorter ASI.

While further results on progress from selection in this study are awaited, Machado and Paterniani (1988) have reported satisfactory improvement in the N use efficiency of a population after one cycle of MS under low N levels. At CNPMS, Sete Lagoas, Brazil, efforts are underway to identify traits that would aid in selection of genotypes more efficient in N absorption and utilization. Traits receiving attention are root length, capacity for assimilation of free ammonium ions, and glutamine synthetase activity. Genetic variation for the traits has been observed and selection has been practiced for three cycles in 'Nitroflint' and 'Nitrodent' populations. Preliminary results suggest excellent progress from selection in N uptake and utilization capacity and yield (Machado _et_ _al_., 1990).

8. CIMMYT's Quality Protein Maize (QPM) Program:

QPM maize possesses the recessive allele, o_2, that confers significantly higher levels of lysine and tryptophan, two essential amino acids that are important in the diets of humans and monogastric animals. At the beginning of 1970, CIMMYT initiated a breeding program to solve problems associated with the QPM maize that hindered use of such cultivars by the farmers. These problems included reduced grain yield, soft and chalky kernel appearance, greater vulnerability to ear rot organisms, more severe damage by stored-grain insects, and slower drying following physiological maturity. Donor stocks were developed with vitreous endosperm and protein quality similar to that of soft endosperm types, exploiting modifiers of the o_2 locus. A modified backcrossing scheme was used that permitted continuous accumulation of modifiers and use of the most advanced versions of the recurrent parents. The maize germplasm with o_2 locus and modified kernel types was later termed quality protein maize (QPM). Thirteen gene pools, 10 populations, and hundreds of OPVs have been developed using modified backcrossing and recurrent selection for distribution and use by the national programs. During 1985, CIMMYT initiated development of QPM inbred lines and hybrids to exploit heterosis, ensure seed purity, and reduce effect of contamination (CIMMYT, 1981; Vasal et al., 1984; Bjarnason, 1990).

Various QPM variety trials were conducted by CIMMYT during 1988, at 80 sites in Africa, Asia, and Latin America. In 15 of the 80 sites where the trials were conducted, the yield of QPM varieties was higher ($P<0.05$), in 54 cases equal, and in 11 cases lower

($P<0.05$) than those of normal hybrids and varieties used as checks.

During 1988, CIMMYT personnel evaluated single cross QPM hybrids developed from S_4, S_5, and S_6 lines in 11 different diallel trials at various sites. In all trials, the superior QPM single crosses out-yielded the best normal checks. The superior five white QPM single crosses yielded 37-49% higher than QPM varieties, 5-14% higher than the normal hybrids, and 32-43% higher than local checks included in the trials (means of 4 sites). The yellow QPM single crosses yielded 18-25% higher than QPM varieties, 1-7% higher than normal hybrids, and 11-17% higher than local checks included in the tests (means of 3 sites).

A trial involving late white tropical QPM materials was conducted at five sites to compare QPM materials with local normal checks (Bjarnason, 1990). Included were three QPM double crosses, three QPM three-way crosses, one QPM family hybrid, one QPM EV along with a local normal check. One QPM hybrid yielded more than the best local check at each site and three QPM hybrids out-yielded the best local checks across sites. The QPM materials were generally earlier than normal materials (Table XIII).

Table XIII.

Comparison of white tropical QPM materials to a local normal check at five international sites in 1989.

Materials	Yield	Days to silk[a]	Ear ht[b]	Ear rot
	t/ha	no.	cm	%
Double cross 2 Q	7.95	58	127	5.6
Triple cross 2 Q	7.74	60	114	2.1
Double cross 1 Q	7.72	66	121	3.5
Triple cross 3 Q	7.67	64	134	6.9
Family hybrid Q	7.53	59	125	6.3
Triple cross 1 Q	7.44	61	138	4.4
Capinopolis 8563	7.07	61	123	8.8
Double cross 3 Q	6.75	62	129	9.2
Las Acacias 8562	6.36	65	110	6.1
Best Local Check	7.26	71	135	3.9
LSD (P<0.05)	0.58			

[a] Days to 50% silking from 3 sites.

[b] Ear height from 4 sites.

Another trial was conducted with late tropical yellow materials at five sites. One QPM hybrid yielded equal to or more than the best local normal check at each site. No difference was observed in the performance of QPM and normal hybrids (checks) (Table XIV). These results indicate that QPM hybrids that have been developed are fully competitive with normal hybrids.

Table XIV.

Comparison of yellow tropical QPM materials to a local normal check at five international sites in 1989.

Materials	Yield	DF	Ear ht	Ear rot
	t/ha	no.	cm	%
Double cross 2 Q	5.54	49	113	8.5
Double cross 2 Q	5.47	53	111	10.5
Double cross 1 Q	5.36	51	116	7.2
Double cross 3 Q	5.26	50	114	11.2
Triple cross 3 Q	5.23	53	116	6.5
Triple cross 2 Q	5.14	51	108	6.6
Across 8565	4.57	52	102	12.7
S8766 Q	4.39	51	99	8.0
Poza Rica 8666	4.35	52	104	10.1
Best Local Check	5.46	56	121	9.2
LSD ($P<0.05$)	0.32			

CIMMYT has discontinued improvement of QPM populations but will continue to develop QPM lines tolerant to ear rots and leaf diseases to be used in hybrids and synthetics by countries that demonstrate interest in such materials. In the future, use of RFLPs to identify modifiers may enhance the efficiency of QPM breeding programs (Bjarnason, 1990).

9. Selection for Disease Resistance:

A collaborative program of disease resistance was initiated in 1974 to concentrate on downy mildew, corn stunt, and streak virus. Six national maize programs entered this collaborative project: Thailand and the Philippines for downy mildew resistance, El Salvador and Nicaragua for corn stunt, and Tanzania and Zaire for maize streak. Recurrent selection for improved disease resistance was practiced in three broad-based tropical populations, tropical late white dent (TLWD), tropical yellow flint-dent (TYFD), and tropical intermediate white flint (TIWF). Alternate cycles of selection were carried out in disease-prone areas in the collaborating countries to identify resistant families, and in Mexico to improve agronomic characters of the resistant selections. Plantings were made at the time of highest disease incidence in the collaborating countries to provide data for selection and recombination of resistant families in Mexico.

Four cycles of S_1 selection and recombination for downy mildew and corn stunt resistance had been completed by 1980. Trials for corn stunt were planted in Guatemala, El Salvador, Nicaragua, Panama, the Dominican Republic, and Mexico and those for downy mildew were planted in Honduras, Venezuela, Nepal, Thailand, the Philippines, and Mexico. Results showed that the advanced cycles of selection of these populations had improved disease resistance and higher yield under both disease-free and disease-pressure situations. Other agronomic characters such as plant and ear height and maturity have improved, as well (Table XV) (De Leon, 1982).

Table XV.

Progress in improving resistance to downy mildew and corn stunt diseases in collaborative research, 1980.

Disease and Population tested	Cycle	Disease	Yield	Plant ht	Days to silk
	no.	%	t/ha	cm	no.
Downy Mildew (Thailand):					
Trop. Interm. White Flint	CO	41.4	3.84	185	68
	C4	0.0	4.40	160	66

Table XV. Continued.....

Trop. Yellow Flint-Dent	CO	67.4	2.68	199	68
	C4	2.6	4.49	183	66
Stund desease (El Salvador):					
Trop. Interm. White Flint	CO	30.6	3.34	206	49
	C4	21.8	4.12	200	49

S_1 lines from the last cycle of selection of the three populations were screened for their reaction to streak virus at IITA and several lines showed good to excellent resistance (M. Bjarnason, 1991, personal communication). Improvement of tolerance to stunt was reinitiated in a population formed by intermating eight EVs from population 73, using S_1 recurrent selection. The synthetic formed during C3 was superior to previously stunt tolerant EVs across seven locations during 1990 (H. Cordova, 1991, personal communication).

Nearly 20 varieties released and grown in Nicaragua, El Salvador, Honduras, Mexico, Venezuela, Philippines, Nepal, Vietnam, and Indonesia trace their origin to this germplasm (Cordova et al., 1989; C. De Leon, 1990, personal communication).

Selection for DMR was also practiced and progress made in three maize populations (Populations 22, 28, and 31) improved through international testing, by the CIMMYT's Asian Regional Maize Program (ARMP) based in Thailand. Four new maize populations (EW-DMR, EY-DMR, LW-DMR, and LY-DMR) have been developed and are being improved for DMR, using S_1-S_2 recurrent selection. Bulks of C0, C1, C2, and C3 of all four populations were evaluated for DM incidence in disease nurseries and for agronomic traits under disease-free conditions in Thailand and the Philippines during 1990. Results indicated that the recurrent selection scheme resulted in simultaneous improvement of levels of DMR (-11**% per cycle) and grain yield (507** kg per cycle) over the four populations (De Leon and Granados, 1991).

Techniques have been refined at CIMMYT for inoculation with: (1) *F. moniliforme* and *D. maydis* ear and stalk rots, (2) *E. turcicum*, and *B. maydis* leaf diseases, and (3) stunt disease, etc., (CIMMYT, 1979; 1981). Studies have been conducted to determine progress from selection for ear and stalk rot resistance (De Leon and Pandey, 1989). They reported that the MER selection scheme was effective in increasing grain yield (2.50**%), resistance to ear rot (-0.90**%) and stalk rot (-1.66**%), and reducing days to silking (-0.15**%) and plant height

(-0.35^{**}%) (Table VII). Ceballos *et al*. (1991) reported 19 and 6% improvement in the resistance to *E. turcicum* (Pass) and *P. sorghi* per cycle after four cycles of combination of FS and S_1 selection in eight subtropical materials. They concluded that resistance to *E. turcicum* was highly heritable and that breeding methodology employed was effective in improving resistance to the two diseases. Significant GCA and SCA effects have been observed for resistance to *P. maydis* (Ceballos and Deutsch, 1989). The trait is under control one to two dominant genes in the most resistant lines. They also reported additive gene effects for resistance in a related study.

10. Selection for Insect Resistance:

At CIMMYT, four species of insects, SWCB, SCB, FAW, and corn earworm (CEW) are mass reared for artificial infestation of over 100,000 plants per year. Resistance breeding is done in the fields with emphasis on reducing damage from larvae. All artificial infestations are carried out with bazooka at the appropriate stage of plant development (Mihm, 1989).

A multiple-borer-resistance population 590 (MBR) has been developed with the objective of recombining sources of resistance to temperate and subtropical stalk borers such as *O*. *nubilalis* (ECB), SWCB, SCB, *C*. *partellus*, *S*. *calamistis*, *E*. *saccharina*, and *B*. *fusca*. Multiple resistance provides the poor farmers in the tropics protection against multiple insects present in their fields. Inclusion of germplasm with diverse resistances assures a more durable and higher level of resistance.

Two hundred FS families of MBR were tested at six locations for tolerance to six insect species. All families were either resistant or intermediate in their reaction to ECB and *C*. *partellus*, all but 1% of the families were either intermediate or resistant to *Diatraea* spp., and 77% of the families were either intermediate or resistant in their reaction to *B*. *fusca*. Between 18 and 52% of the families also rated resistant to FAW. Approximately 39% of the families were resistant to one species, 24% to two species, 9% to three species, 2.5% to four species, and 0.5% to five species. None was resistant to all six species (Smith *et* *al*., 1989).

Studies have also been conducted that relate to genetics of insect resistance. Sosa *et* *al*. (1990) evaluated 8 cycles of modified FS selection in the population Antigua-Veracruz 181 for leaf feeding and tolerance to FAW at several sites. They reported 5.5%

yield increase per cycle under infestation. Since there was no change in leaf feeding, and selection of progenies in each cycle was largely based on yield under infestation, they concluded that the progress was due to a change in tolerance of the population to FAW. Thome et al. (1990) observed high GCA effects for resistance to ECB, SWCB, and SCB in three resistant lines derived from the MBR pool and concluded that resistance in these lines was largely dominant in nature. De Leon et al. (1990) have reported on RFLP analysis of six resistant lines from the MBR pool and one susceptible line. Six chromosome regions of the genome were similar to that of the resistant parent, particularly within chromosome 2; and several regions in chromosomes 4 and 6 were similar to those in the susceptible parent.

A multiple-insect-resistant tropical population 390 (MIRT) has also been developed with some of the sources of resistance included in the MBR pool and with insect resistant selections from CIMMYT's tropical populations and pools. It is assumed that the MBR population would probably never be the best source of resistance to tropical insect species. MIRT is expected to possess disease resistance and agronomic characters needed in maize germplasm for the lowland tropics. Resistance to SCB and FAW are the traits under selection in the population. Breeding for insect resistance also focuses on evaluation of germplasm bank accessions for tolerance to various insect species, on improving resistance to CEW in highland maize germplasm, and on transferring genes for borer resistance from Tripsacum spp. (CIMMYT, 1988).

EVs derived from MBR were recently compared with other insect tolerant materials in a 10-entry trial in paired infested/protected row plots. Six replications were used at each of several locations in the USA, Canada, and Mexico. Results indicated that: resistant materials had lower leaf-feeding ratings and suffered lower yield reductions than the susceptible materials, MBR EVs were equal or superior to the resistant checks in performance, and resistant materials could be used as sources of resistance to multiple borer and armyworm pests (Table XVI)(J. Mihm, 1991, personal communication).

Table XVI.

Performance of EVs derived from MBR, when artificially infested with ECB, FAW, SCB, and SWCB larvae at different sites in the USA, Canada, and Mexico in 1990.

Materials	Leaf-feeding ratings				Yield reduction
	ECB[a]	FAW[b]	SCB[c]	SWCB[d]	Inf. vs. prot.[d]
	----------1-9[e]			-------------	%
Font 6230	6.5	8.2	7.5	8.1	39.7
Ki3/Tx601	6.2	8.0	4.3	7.2	26.6
B73/Mo17	5.9	8.1	7.2	8.1	43.8
Pioneer 3184	5.0	7.0	6.9	7.6	31.8
MBR-ECB	4.0	5.8	3.5	5.7	11.5
MBR-Chilo	3.6	6.0	3.6	5.6	17.9
MBR-SWCB	3.6	6.0	3.9	5.6	23.5
MBR-SCB	3.5	6.0	3.9	5.7	3.3
MBR-All bugs	3.5	5.4	3.9	5.7	9.2
P47s3/Mp78:518	3.3	5.9	4.1	4.9	12.8
Susc. check	7.3	7.0	---	7.4	26.6
Res. check	3.8	5.5	---	4.6	18.1

[a]1Means of four environments.

[b]Means of three environments.

[c]Means of one environment.

[d]Means of two environments.

[e]1=highly tolerant; 9=highly susceptible.

11. Selection for Tolerance to Soil Acidity:

Because Al and P stresses tend to occur together, development of improved cultivars should involve simultaneous selection for tolerance to the two stresses. Fortunately, genetic variation has been reported for tolerance to both stresses. CIMMYT at Cali, Colombia, has been improving a maize population, SA-3, for tolerance to soil acidity for about 20 cycles. The population was developed in the late 1970s at Santander Quilichao, Colombia. During 1977, 192 materials of diverse origins were planted in single-row plots at 45 and 75% aluminum saturation. At harvest, 70 ears were selected, and 45 materials were observed to have good plant development. In 1978, remnant seed of these 45 materials was planted as females, and a bulk mixture of seed from the 70 selected ears as males, in a HS recombination block. The resulting population was improved using MER selection scheme at 45 and 75% Al saturation and 6-7 ppm P (G. Granados, 1991, personal communication). The population, and the varieties derived from it, show higher levels of tolerance and good agronomic attributes (S. Pandey, unpublished).

Research was initiated in 1985 to develop two white (SA-6 and SA-7) and two yellow populations (SA-4 and SA-

5) tolerant to acid soils. National program materials with tolerance to acid soils and CIMMYT materials that performed well in Latin America, Asia, and Africa were obtained. In 1986, 36 materials were selfed and sibbed at Cali, Colombia, and 613 yellow and 618 white S_1 lines were selected. During 1987-88, the materials were evaluated in acid soil trials in Brazil, Colombia, Indonesia, and Philippines to determine whether some of them might be of immediate use to cooperators and to get a better idea of their characteristics. During 1987 at Cali, the S_1 yellow lines were topcrossed to two yellow heterotic lines from the Colombian national program and the white S_1 lines with two white heterotic lines from this program.

On the basis of the performance of the lines in the topcross formation block, topcrosses of 250 lines from each of the two groups were harvested for further evaluation. In the second season of 1987, the 613 yellow and 618 white lines were evaluated under different levels of Al and P concentrations and under nonacid soil conditions. The topcrosses were evaluated at Santander Quilichao in acid soils and at Cali in non-acid soils during 1987. In 1988, the four populations were developed on the basis of the lines' performance and their heterotic patterns. The two white populations form a heterotic pair as do the two yellow ones.

The populations are evaluated in the field under Al saturations ranging from 40 to 75% and P levels ranging from 5 to 12 ppm at Carimagua, and Santander Quilichao in Colombia. In addition, the materials are evaluated under acid soil conditions in Brazil, Indonesia, Peru, Philippines, Thailand, Venezuela, among others. Testing also takes place under normal soil conditions to facilitate the accumulation of genes for yield potential at the same time that acid soil tolerance is being improved. Where acid soils occur, this germplasm should perform significantly better than susceptible genotypes, but where they do not, they should still be highly responsive to favorable soil conditions. Two cycles of FS selection have been completed in SA-4, SA-5, SA-6, and SA-7.

E. HYBRID DEVELOPMENT AT CIMMYT

Many national programs have initiated hybrid development activities to satisfy needs of their farmers. To serve such national programs better, CIMMYT initiated a program in 1985 to develop new germplasm products for hybrid development and to accumulate and publish information about the utility for hybrid development of the tropical and subtropical materials of CIMMYT (Vasal *et al.*, 1987). Eight diallel trials were developed based on adaptation, maturity, grain color, and protein quality of materials to study combining ability of CIMMYT materials and to determine their heterotic patterns. The evaluations were made at several locations in Mexico, the USA, and various countries in Central and South America and Asia. Five highest yielding crosses in each diallel trial were selected. The high parent heterosis in these five crosses across the diallel trials ranged from 2 to 19%.

CIMMYT has also developed and evaluated several types of hybrids during the last several years. Many of these hybrids are superior to the checks (OPVs and hybrids) included in the trials by the national programs (Table XVII).

Table XVII.

Performance of different types of hybrids developed and evaluated by CIMMYT in several environments during 1986-1990[a].

Types of hybrids	Yield	Superiority over checks	High-parent heterosis
	t/ha	---------------%---	-------------
Single Crosses	7.2	29[b]	--
Double Crosses	7.1	20[c]	--
Three-way Crosses	7.6	28[b]	--
Double Topcrosses	7.6	---	25
Topcrosses	7.9	---	41
Inter-family Hybrids	7.2	---	33
Inter-synthetic Hybrids	6.6	---	13

[a] S.K. Vasal, 1991, personal communication.

[b] Checks were OPVs.

[c] Checks were hybrids.

Crossa et al. (1990b) evaluated diallel crosses among seven tropical late yellow populations in seven environments and found Suwan-1 and Population 24 to have the highest mean yield in crosses and high heterosis. Populations 28 and 36 had a high cross mean but relatively lower heterosis. They recommended interpopulation improvement involving populations 24 and 36.

Beck et al. (1990) evaluated diallel crosses among 10 CIMMYT populations and pools with early and intermediate maturity at five locations. General combining ability was significant for all traits and SCA was significant for ear height only. Population 49 x Population 26 and Population 26 x Pool 21 provided high-parent heterosis of 9.6 and 7.3%, respectively. Pool 22 showed the highest GCA effects (0.37t/ha) and the only cross with significant SCA effect (6.7%) involved Population 23 and Pool 20. They recommended hybrid development involving Population 23 and Pool 20 for white materials and Population 26 with either Pool 21 or 22 for yellow materials. CIMMYT maize program is currently involved in development and improvement of heterotic populations tolerant to inbreeding depression and identification of new heterotic patterns (S.K. Vasal, 1991, personal communication).

Heterotic patterns of various CIMMYT materials are summarized in Table XVIII.

Table XVIII.

Possible heterotic combinations for some CIMMYT populations.

Population	Possible heterotic partner(s)
21	Pops. 25 and 32; Pool 23
22	Pops. 25 and 32
23	Pop. 49; Pool 20
24	Pops. 27, 28, and 36; Suwan-1
25	Pops. 21, 22, 27, 29, 43 and 44; Pool 24
26	Pop. 31; Pool 21
27	Pops. 24, 25, 28, and 36; Suwan-1
28	Pops. 24 and 27; Suwan-1
29	Pops. 25 and 32
31	Pop. 26; Pool 22
32	Pops. 21, 22, 29, and 44
33	Pop. 45
34	Pops. 42 and 47; Pool 32
36	Pops. 24 and 27
42	Pops. 34, 43, 44, and 47

Table XVIII. Continued.....

43	Pops. 25, 42, and 44
44	Pops. 25, 32, 42, 43, and 47; Pool 32
45	Pop. 33; Pool 33
46	Pop. 48; Pool 30
47	Pops. 34, 42, and 44
48	Pop. 46
49	Pop. 23; Pool 19

F. RECURRENT SELECTION AND GENOTYPE AND GENOTYPE X ENVIRONMENT VARIANCES

Gardner et al. (1990) calculated genotype, genotype x environment, and error variance components of CIMMYT's 11 tropical maize populations, using data from international progeny trials (Tables XIX and XX). Test sites and their numbers were generally different for different cycles of selection. The results indicated no reduction in either genotypic or genotype x environment interaction variances in any of the populations. The broad genetic base of CIMMYT populations, low initial frequency of desirable alleles, low selection intensity, introgression of additional germplasm, extremely diverse environments used during different selection cycles, etc., were cited as possible explanations for the results obtained.

Table XIX.

Genetic components of variance for each cycle of selection in eleven CIMMYT populations undergoing full-sib family recurrent selection.

	Cycles						
Population	0	1	2	3	4	5	6
21	.1350	.0664	.1504	.2414	.2164	-.1113	
22	-.4479	.1806	.1184	.1194	.2402	.1032	.2968
24	.3461	.2311	.0961	.2579	.2393	.2180	.2409
27	.2106	.1844	.1223	.1534	.2562	.1760	.3167
28	.2393	.1445	.0747	.2362	.2142	.0870	
29	.1131	.1011	.0807	.1333	.1938	.1442	
32	.2665	.1400	.0060	.1979	.1148		
35	.1440	.0867	.2310	.1643	.1183		
36	.1810	.1324	.1636	.0852	.1738	.1439	
43	-.0116	.2009	.2637	.1810	.1073		
49	.1970	.1979	.0986				

Table XX.

Genotype x environment interaction components of variance for each cycle of selection in eleven CIMMYT populations undergoing full-sib family recurrent selection.

	Cycles						
Population	0	1	2	3	4	5	6
21	.6763	.1954	.5364	.2103	.2973	3.8075	
22	5.6269	.3247	.0774	.1862	.9319	.4116	.2882
24	.0800	.2529	.1698	.2147	.0669	.2148	.1006
27	.0843	.1958	.1426	.0963	.3387	.0995	.0849
28	.2604	.1396	.3232	.1828	.2127	.2819	
29	1.7417	.8230	.1629	.3798	.1650	1.0064	
32	.4291	.0919	1.9472	.1480	.2600		
35	.1228	.0839	.0803	.3231	.1266		
36	.1196	.2637	.2059	.1685	.0093	.1193	
43	2.2593	.1248	.0620	.2140	.2924		
49	.1153	.1494	.1152				

Weighted mean estimates (weights used were inverse of the variance of each estimate) were used to estimate mean yield, and genotype, genotype x environment, and error variances for the 11 populations by Gardner _et_ _al_. (1990), using data pooled over cycles of selection (Table XXI). The results indicate that good data from two replications at six sites would result in satisfactory progress from selection. More replications could not be justified. With data from only three locations, expected gains would be greatly reduced. They emphasized the need for classification of environments based on the use of the resulting products and for collecting good quality data for maximizing progress from selection.

Table XXI.

Estimates of means, components of variance, and expected progress from full-sib family recurrent selection in 12 CIMMYT populations.

Population	Mean[a]	Components of variance[a]			Expected gain (%)[b]	
		Error	G x E	Genotypic	6 env.	3 env.
21	5.09	.8515	.3712	.1422	3.49	2.86
22	5.38	.8111	.2287	.1375	3.39	2.83
24	4.97	.6736	.1760	.1955	4.86	4.26
27	4.54	.5997	.1297	.1771	5.13	4.52
28	4.75	.7259	.2138	.1433	4.04	3.41
29	5.24	.7449	.3102	.1108	2.92	2.38
32	4.08	.6578	.1704	.1611	5.24	4.42
35	4.92	.5525	.1150	.1286	3.89	3.37

Table XXI. Continued.....

36	5.19	.6598	.1486	.1481	3.92	3.37
43	5.56	.9555	.2194	.1705	3.75	3.17
48	6.09	.5176	.1282	.1399	3.33	2.90
49	5.05	.5783	.1269	.1440	4.04	3.51

---

[a] Weighted means where weights were the inverses of the variances of the parameters estimated each cycle of selection.

[b] Expected gains from selection calculated assuming the ratio of dominance variance to additive genetic variance to be 0.9377 (average of 99 maize genetic studies reported by Hallauer and Miranda, 1988) and a selection intensity of 20%.

Pandey et al. (1986, 1987, 1991) used the stability analysis of Eberhart and Russell (1966) to analyze the data from cycles of selection trials of late and medium maturity CIMMYT populations and from the trial of EVs derived from the original and the latter cycles of selection from most of the same populations. The deviations from regression were generally nonsignificant (except in the case of medium maturity materials where they were significant at $P=0.05$), and are not reported here. The b values for C4/C5 of the late materials were significantly lower than those for C0 (Table XXII). The most recent cycles of selection had lower b values than C0 in the case of six of the eight populations. The last cycles had higher yields across the environments as well.

The advanced cycles of selection yielded higher than C0 in 15 cases out of 16 in low-yielding environments and in 21 cases out of 32 in high-yielding environments.

In the medium maturity materials, the b values decreased significantly from C0 to C2 and then increased again (Table XXII). In two of the four populations the advanced cycles of selection averaged higher yields and lower b's than C0. In this study as well, the advanced cycles of selection yielded more than C0 in 11 cases out of 12 in low yielding environments and 12 cases out of 16 in high yielding environments.

Table XXII.

Stability for yield in several tropical maize populations.

Late tropical materials (means 8 pop. and 6 locs.)			Medium maturity materials (means 4 pop. and 7 locs).		
Cycles	Yield	b	Cycle	Yield	b
	-----t/ha------			------t/ha------	
C0	5.88	1.04	C0	4.89	1.04
C2	5.88	1.01	C1/C2	4.96	0.92

Table XXII. Continued.....

C4/C5	6.23	0.96	C4/C5	5.32	1.04
LSD (P<0.05)	0.11	0.04		0.14	0.06

The regression values of Across EVs derived from C3/C4 were lower than those from Poza Rica and Across EVs derived from C0 and Poza Rica EVs derived from the last cycle ($P<0.01$). The results indicate that EVs developed from advanced cycles of selection of populations undergoing recurrent selection yield more ($P<0.01$) and are more stable ($P<0.01$) than those developed from the original cycle (Table X) (Pandey et al., 1991). Gardner et al. (1990) attributed the improvement in the stability to elimination of deleterious genes, shorter plant height, higher harvest index, and improvement in resistance to biological and environmental stresses.

VII. SOME CONSIDERATIONS IN ORGANIZING AN EFFICIENT MAIZE IMPROVEMENT PROGRAM

Recurrent selection should be an integral part of any applied maize breeding program whether the ultimate product is an improved variety or some kind of hybrid.

The systematic accumulation of favorable alleles and favorable combinations of alleles in advanced cycles makes them superior sources of new inbred lines for use in hybrids as well as superior sources of new varieties for release to farmers.

Eberhart *et al*. (1967) suggested a comprehensive breeding system in maize based on experiences in Kenya, which was further discussed by Sprague and Eberhart (1977). Such a comprehensive system has three distinct phases: 1) the development of two or more breeding populations from diverse sources so that the population per se and the population-cross mean(s) will be at the highest level possible and the populations will have maximum additive genetic variation within each, 2) continuous population improvement by an effective recurrent selection program, and 3) the development of superior hybrids from each cycle of selection by an efficient and systematic procedure. Gardner (1986) discussed the development of breeding populations and the integration of population improvement with hybrid development activities to develop superior maize cultivars for the tropics.

In developing countries where the release of a new improved variety may be the most useful end product, intrapopulation recurrent selection provides a steady source of new varieties at each cycle of selection. Many such new varieties have been developed from superior FS families extracted from improved CIMMYT populations (Pandey et al., 1986, 1987). These populations have been involved in FS family recurrent selection programs (or modification thereof) for several cycles. Unfortunately, most CIMMYT populations appear to have been developed from very broad germplasm resources without regard for heterotic patterns. Hence, there is little interpopulation heterosis observed in crosses among them (Crossa et al., 1990b; Beck et al., 1990). Nevertheless, considerable heterosis has been reported between lines derived from the same and different CIMMYT maize populations (Han et al., 1991).

As developing nations advance and become more interested in hybrid programs, heterotic patterns among populations available becomes increasingly more important. Heterotic patterns among maize races, varieties or other open-pollinated populations from tropical and sub-tropical countries have been observed (Crossa et al., 1990a; Gardner and Paterniani, 1967; Castro et al., 1968; Paterniani and Lonnquist, 1963). Heterosis estimates of 100 to over 200% above the better parent are common. Such information is useful in forming two or more breeding populations to which reciprocal selection might eventually be applied. Such reciprocally developed populations can be improved to serve as useful resources for new varieties, and will be far more useful for developing inbreds and hybrids. The main reason that reciprocal selection systems have not been used by CIMMYT is related to the primary objective, which has been improved varieties, and the cost of simultaneously improving two populations compared to one.

Comparisons between intrapopulation and reciprocal interpopulation selection methods indicate that selection in early cycles is for additive genetic effects with partial to complete dominance in both systems. They seem to be equally effective in increasing the interpopulation cross mean (Moll and Stuber, 1971; Odhiambo and Compton, 1989). At the same time, intrapopulation selection is more effective in improving population means, and S_1 family selection is definitely more effective in reducing inbreeding depression and improving means of selfed progenies (Odhiambo and Compton, 1989). S_1 family selection is also very effective for improving insect and disease resistances and environmental stress tolerances. Therefore, since reciprocal selection programs are more difficult and costly to run, it seems wise to use S_1 family selection in each of the two populations in the early cycles and switch to reciprocal FS selection after about five cycles when gains due to overdominance and dominance types of epistasis are likely to become relatively more important. For traits that are highly heritable, a few cycles of intrapopulation selection will be highly effective.

Jones _et_ _al_. (1971) provide evidence to support the choice of reciprocal FS over reciprocal HS selection. An additional advantage is that new reciprocal pairs of S_1 lines for further development and use in hybrids are a natural spinoff each cycle of selection. However, no one has compared the systems on the same population.

In international work, where it is sometimes difficult to conduct good evaluation trials of S_1 families in early cycles of selection, use of FS family evaluation and selection could be substituted for the S_1 family system providing a generation of inbreeding with selection among plants within S_1 families is used as described by Pandey _et_ _al_. (1986). This should result in improved tolerance to inbreeding where recurrent selection is fully integrated with a hybrid program.

In basic genetic studies designed to obtain information about population parameters and how they are influenced by selection, it is essential to work with closed populations. However, in any maize improvement program where the ultimate objective is release of a new cultivar, there is no reason to keep a breeding population closed. New promising germplasm can be introgressed continually as has been done at CIMMYT. In reciprocal programs, such additions must take into account heterotic patterns.

VIII. CONTRIBUTION OF RECURRENT SELECTION TO MAIZE PRODUCTION IN THE TROPICS

The studies to determine contribution of genetics and plant breeding in increasing maize yields in the tropics are limited. As has been previously mentioned, approximately 53% of the total maize area in the developing countries is planted to improved materials -- 39% to hybrids and 14% to open-pollinated varieties (CIMMYT, 1990). While hybrids have been reported to yield about 11% more than varieties in Mexico and Central America, the yields of the two types of germplasm are indistinguishable in many environments. In fact, in high stress areas, varieties may outyield hybrids (CIMMYT, 1987). Some studies have compared improved varieties and hybrids with those of the farmers' cultivars in both farmers' fields and at experiment stations. They may provide an indication of the contribution of superior germplasm to increased maize yields in the tropics.

Maize scientists of ICA, Colombia, compared a local maize cultivar ('Native'), with the local cultivar contaminated with improved cultivars ('Regional'), the Regional improved through recurrent selection ('Improved Regional'), an improved OPV ('Improved Variety'), and a hybrid, at 10 sites in different seasons, with a total of 27 environments (F. Arboleda, personal communication, 1990). Five of the sites were in the lowlands, three in the medium altitude areas, and two in the highlands. The materials evaluated at each site were adapted to that ecosystem.

Table XXIII.

Performance of Native, Regional, Improved Regional, Improved Variety, and hybrid in 27 environments at 10 sites during 1986-1988 in Colombia.

Type of Material	Yield at altitudes			
	Low[a]	Medium[b]	High[c]	Mean
	t/ha			
Hybrid	3.86	5.53	5.21	4.81
Improved Variety	4.00	4.77	5.04	4.64
Improved Regional	2.88	4.33	4.40	3.85
Regional	2.81	2.95	3.74	3.32
Native	2.22	2.24	2.47	2.36
LSD ($P<0.05$)	0.18	0.32	0.25	0.18

[a] Means of 13 environments.

[b] Means of 6 environments.

[c] Means of 8 environments.

Averaged over environments, the Native yielded significantly less than the other types (Table XXIII). Although, no differences were observed in the performance of the Improved Variety and the hybrid, both were superior to Native, Regional, and Improved Regional cultivars. The Improved Regional was superior to the Regional in yield. This study also demonstrated the improvement of farmers' cultivars through chance introgression of improved germplasm in them, an indirect contribution of superior germplasm to yield improvements. Although the trials were conducted at experiment stations, the yields ranged from 1.42 to 6.00 t/ha across environments, indicating that a range of environments was sampled. No clear differences were detected in yield patterns of the genotypes for the different groups of altitudes sampled.

In Venezuela, scientists have examined maximum yields of varieties and hybrids from different decades at experiment stations, showing approximately 50 kg/ha/yr (Table XXIV) increases in yields of the genotypes during 1930-1980 (A. Bejarano, personal communication, 1990). The national maize yields ranged from 34-39% of the experiment station yields, averaging about 35%, during the period 1957 through 1985.

Table XXIV.

Performance of maize varieties and hybrids developed in different periods in Venezuela.

Years	Varieties	Hybrids
	---------------t/ha	-----------------
1930 (Locals)	2.5	--
1940	3.0	--
1950	3.5	4.5
1960	4.0	5.0
1970	4.5	5.5
1980	5.5	6.0

Sanchez (1990) summarized results of about 200 trials conducted largely in the farmers fields in the lowlands of Peru and Bolivia during the 1970s and 1980s and compared performance of different types of cultivars (Table XXV). Unfortunately, it is not possible to determine the relative contribution of germplasm and improved management in the yield improvements reported in the study.

Table XXV.

Performance of different types of maize cultivars during the 1970s and 1980s in the lowland areas of Peru and Bolivia. The results are based on 200 trials conducted in Peru and 150 trials in Bolivia, largely in the farmers' fields.

	-----Peru----		----Bolivia----	
Types of Germplasm	1970s	1980	1970s	1980s
	-----------t/ha-----------			
Commercial Hybrids	4.3	7.5	7.5	7.2
Improved Varieties	4.6	8.2	---	6.1
CIMMYT Varieties	4.7	7.2	8.0	7.8
Varietal Crosses	5.0	8.2	5.0	5.0
Nonconventional Hybrids[a]	---	11.2	---	---
Topcrosses	---	11.3	8.5	9.0
Conventional Hybrids	---	12.0	---	---
Checks	3.0	6.5	4.0	5.2

[a] One or more parents are noninbreds.

The superiority of maize types during the 1980s ranged from 53 to 98% over that in the 1970s in Peru and only slight superiority was detected in Bolivia. The most dramatic improvement occurred in the performance of local checks, indicating high adoption rate of improved most dramatic improvement occurred in the performance of local checks, indicating high adoption rate of improved germplasm, particularly in the coastal and jungle areas of Peru. The data demonstrate the differences in the efficiencies of different national programs in developing superior germplasm for their farmers, in addition to showing superiority of improved materials over farmers' cultivars.

An on-farm maize trial conducted at 10 locations in Ghana showed that improved germplasm plus recommended management practices yielded 4.20 t/ha compared to 1.45 t/ha yield of farmers' varieties under their own practices (Akposoe and Edmeades, 1981). In their study, improved germplasm contributed 21%, fertilizer use (90:60:60 kg $N:P_2O_5:K_2O$) 54%, and improved weed control 7% of the yield increases. In a similar study over a period of 10 years, Chutkaew and Thiraporn (1987) reported that improved germplasm contributed 37%, increased fertilizer use 43%, and improved weed control 20% of the yield increases in Thailand.

The current values accepted for maize yield increases in the tropics might be biased if we accept the idea that more maize is grown in marginal environments (environments where maize yields are reduced to 10-40% of their potential productivity) each year. More productive areas are used for higher return crops and activities, or to social circumstances (Edmeades and Tollenaar, 1990). An example of this phenomenon is found in Colombia. During 1972, 64,500 ha of maize were grown in Valle de Cauca, with an average yield of 2.5 t/ha (Londono and Andersen, 1975). During the same year, 68,500 ha were planted in Cordoba with an average yield of 1.14 t/ha. Due to expansion of the sugarcane industry and proliferation of social problems in Valle de Cauca, the maize area has gradually declined to 13,900 ha during 1990, with an average yield of 3.56 t/ha. Meanwhile, the maize area in Cordoba has expanded by 101%, to 137,800 ha, in 1990. Average yields in Cordoba, while increasing by 45%, were nevertheless only 1.65 t/ha in 1990 (F. Polania, 1991, personal communication). This displacement of maize from higher yielding to lower yielding environments has been observed in several other tropical countries, lowering yield improvement rates. In Brazil, sugarcane for alcohol production and soybeans have displaced maize from better soils, as well (E. Paterniani, 1991, personal communication). Fortunately, however, yield improvements have been positive in most developing countries.

Edmeades and Tollenaar (1990) estimated that about 70-80% of the yield increases reported in the developing countries are due to changes in crop management practices, principally through increased N use, higher plant densities, and better weed control. Maize yield increases in the developing countries have shown positive correlation (r=0.89**) with the use of improved germplasm and with N (r=0.76**), on a regional basis. The maize production increases through yield improvement in the tropics (45 kg/ha per year) amount to 3.7 million tons of additional maize annually. If only 30% of the yield improvement can be assumed to be contributed by superior germplasm, maize breeding/genetics would be contributing over additional 110 million dollars to the developing countries' economy, annually.

IX. CONTRIBUTION OF TROPICAL MAIZE GERMPLASM TO TEMPERATE MAIZE IMPROVEMENT

Although for many years, introgression of tropical maize germplasm into temperate maize has been suggested as a way to broaden the germplasm base, few successful commercial hybrids in the temperate areas have been reported to include tropical germplasm (Wellhausen, 1965; Goodman, 1985; Hallauer and Miranda, 1988; Castillo and Goodman, 1989). Castillo and Goodman (1989) concluded that factors limiting the use of tropical germplasm in temperate areas include: 1) superiority of existing temperate germplasms and presence of adequate genetic variability in them, 2) poor adaptation of tropical materials in the temperate climate, due mainly to photoperiod sensitivity of tropical materials, 3) more extensive improvement of temperate materials through conventional breeding methods compared to use of tropical germplasm, 4) difficulty in overcoming unfavorable linkages in tropical materials, and 5) limited evaluations of exotic materials in temperate climates. In sorghum, tropical materials have been systematically converted to useful short-statured, photoperiod-insensitive forms, but no such effort has been made in maize.

Some successful use of tropical maize to improve temperate populations has been reported, but more efforts have probably been made that were not reported. Negative results are seldom published, and successful efforts by commercial hybrid companies are not likely to be revealed. Heterosis among temperate and exotic races has been studied (Wellhausen, 1965). Greater genetic variability has been observed in populations containing exotic germplasm. Selection has usually been practiced in populations with 25% or 50% tropical germplasm and with 75% or 50% temperate materials; however, Hallauer and Sears (1972) reported progress from direct selection in 'ETO Composite', and Gardner released to private and public breeders a population derived from CIMMYT's 'Compuesto L-Mc C2' (Antigua Gpo. 2 x Tuxpeno). Nelson (1972) reported on commercial use of inbreds developed using some exotic germplasm in the southern part of the USA. Oyervides et al. (1985) and Gutierrez et al. (1986) have reported lower photoperiod sensitivity in tropical x temperate crosses, compared with tropical materials. Castillo and Goodman (1989) suggested that evaluation of tropical materials under short-day conditions would be superior to that under long-day conditions. Hallauer and Miranda (1988) reported results of a survey of the North Central Region of the USA and found that 25.2% of the public sector populations undergoing improvement contained some exotic germplasm. They suggested that use of exotic germplasm in the research programs of the private sector was perhaps even greater. Several populations with different levels of several tropical materials have been developed and are being improved for adaptability (A. R. Hallauer, 1991, personal communication).

Integration of tropical maize germplasm into adapted maize populations at the University of Nebraska was initiated by Lonnquist in collaboration with tropical maize breeders in the late 1950's and early 1960's. Compton _et_ _al_. (1979) used recurrent selection for adaptability to improve eight such populations and reported average gains of 5.4% per cycle. Gardner's well-adapted population, Compuesto L-Mc C2, abbreviated as 'TA', was used in a diallel cross involving several improved Nebraska populations and the best out of Iowa Stiff Stalk Synthetic and the Nebraska B Synthetic (Crossa, _et_ _al_., 1987). TA was the highest yielding population per se and ranked second in GCA. It combined well with both Lancaster and Reid types and was considered to have good insect and disease tolerance. Extensive use has been made of CIMMYT germplasm in other populations developed by Gardner at Nebraska. They exhibit improved stalk quality, good standability, and insect and disease tolerance.

X. CONCLUSIONS

During the period 1985 to 2000, total annual maize demands are expected to rise by 3.5% in the developing countries - 1.6% for food and 4.9% for feed. The production in developing countries is expected to rise by 3.6% per year. While this growth is lower than 4.0% annual increases during 1970-85, it will still surpass the annual population growth rate of 2% during the same period. In spite of impressive yield improvements and even some increases in maize area during the past decades, developing countries imported over 11 million tons of maize annually during 1986-88 and are expected to be by far the most important source of growth in demand for maize in the world (CIMMYT, 1989).

Most developing countries cannot afford to import maize; hence, getting improved germplasm and improved technologies into use on farms would play a major role in increasing maize production and reducing the need for maize imports. It is recognized that maize production practices in the tropics are generally poor. Improved production practices are bound to contribute more to increased yields initially, but as production practices improve, greater breeding effort is required to increase yields and adapt materials to improved practices. Yield potential of tropical maize should be increased by improving grain production efficiency, measured in time and space. Selection for desirable morphological traits, higher harvest index, reduced ASI, increased efficiency of nutrient uptake and utilization, improved stress tolerances, superior quality traits should all be emphasized in the tropics. Growth in demand for food has encouraged agriculture to expand in marginal area, forcing more and more maize to be grown under stress. This trend is not expected to change soon. Breeding and crop management research should focus on reducing crop losses from weeds, diseases, insects, drought, and toxicities and deficiencies of mineral nutrients. More efficient technologies for germplasm conservation, regeneration, and evaluation must also be developed.

Increased technical capacity of maize scientists in the developing world would enable them to make more efficient use of the available limited resources, by allowing them to choose their germplasm and breeding and testing procedures more effectively. However, little advanced technology development is expected to take place in the developing countries, due mainly to declining budgets for agricultural research. Developing countries would generally be importers and modifiers of advanced technology (computing, biotechnology, etc.). While current breeding methodologies will continue to play the major role in maize improvement in the foreseeable future, biotechnology is expected to particularly aid in genetic improvement of stress tolerance in maize.

Lack of good seed production, processing, storage and distribution facilities in many developing countries has greatly impeded progress in getting improved OPV's and hybrids into the hands of farmers. Thus the impact of superior germplasm developed by maize scientists has been greatly reduced. In developing countries in 1988, the area planted to improved OPV's was 14%, to hybrids 39%, and to local varieties 47% (CIMMYT, 1990). A commercial seed industry will not develop in countries where a profit is not assured. Hence, initially, the public sector must assume a greater role in seed production, storage, and distribution, while at the same time encouraging development of a seed industry. Developing more realistic national policies, pricing the seed of improved cultivars at a level fair to both the farmer and the seed industry, and making superior germplasm available to the private sector should increase goodwill and pave the way for greater private sector involvement in the seed industry. In countries where the private sector has become involved, greater progress has been made in increasing maize production.

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DEDICATION

This chapter is dedicated to the many maize scientists in national programs who have contributed greatly to increased maize yields in the tropics, and particularly to those who have collaborated with CIMMYT maize scientists in the international testing program, which has been mutually beneficial. It is also dedicated to CIMMYT maize scientists for their many contributions to tropical maize improvement and for their dedication to strengthening national programs, training leaders and scientists, and thus improving the lot of poor farmers and consumers in developing countries.

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