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breeding and selection
for drought
resistance in tropical maize

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CONTENTS

iv	Summary
1	Introduction
1	Types of Drought
2	Physiological Factors
4	Breeding for Improved Drought Resistance
7	The CIMMYT Experience
7	Choice in Germplasm
8	Development of Suitable Selection Criteria
10	Intrapopulation Variation and Improvement
12	Evaluation of Progress
16	Conclusions
17	References

11

SUMMARY

Throughout the lowland wet tropics, periodic nonprotracted drought caused by irregular rainfall distribution is responsible for sizable reductions in maize yield. This is particularly true when reduced water availability coincides with the critical stage of crop development--flowering. Such a drought cannot be escaped by genotype maturity or planting date, nor are other species necessarily better adapted. Improving resistance of maize to this particular type of drought, then, could enhance productivity and minimize farmer risk.

From a comparison of sorghum and maize under drought, it appears that sorghum maintains photosynthesis and growth at lower water levels and has more developmental plasticity than maize. Increasing the dry matter available for ear development around flowering may help to reduce the detrimental effects of drought occurring at this critical stage in maize.

Many morphological and physiological characters have been suggested for modification so as to enhance drought resistance in maize. At CIMMYT, one lowland tropical maize population is being improved for drought resistance through a recurrent selection program. Progenies are selected using an index based on grain yield under no stress and stress, leaf elongation rate, interval between anthesis and silking, canopy temperature and leaf area loss during grain filling. Evaluation of the progress after three cycles of recurrent selection shows a significant increase in yield under severe drought conditions. Improvement is approximately 9.5 percent per cycle and is mainly associated with a decrease in the number of barren plants.

Other morphophysiological traits are being evaluated for their effectiveness in changing plant response to drought. Selections for reduced tassel, leaf and height may improve yield under severe stress conditions. Also, through multilocation testing and selection in its Maize International Testing program, CIMMYT has been able to achieve improved tolerance to drought stress.

INTRODUCTION

This paper first defines a specific type of non-protracted drought which affects large areas of the lowland tropics. It compares the drought-resistance mechanisms of sorghum and maize. The ability of sorghum to continue photosynthesis at lower water levels, along with its developmental plasticity, may account for some of its advantages over maize in this type of drought.

It then describes the philosophy of current breeding strategies for drought resistance and reviews techniques used to measure differences between maize genotypes for resistance.

Finally, evidence is given for the effectiveness of recurrent selection for drought resistance using a selection criteria of leaf elongation rate, interval between silking and anthesis, canopy temperature, leaf area loss and grain yield under stress and no stress. This method is being practiced at CIMMYT in one lowland tropical material for the specific type of drought mentioned above.

TYPES OF DROUGHT

Throughout the tropics, periodic drought, caused by irregular rainfall distribution and accentuated by soils with low water-holding capacity, causes sizable reductions in maize yields (Wolf *et al.* 1974). Estimates reveal that drought may account for an average loss of 15 percent of production in tropical areas, even where total rainfall is reasonably high. Further, the probability of yield loss due to drought influences the use and utilization of fertilizer

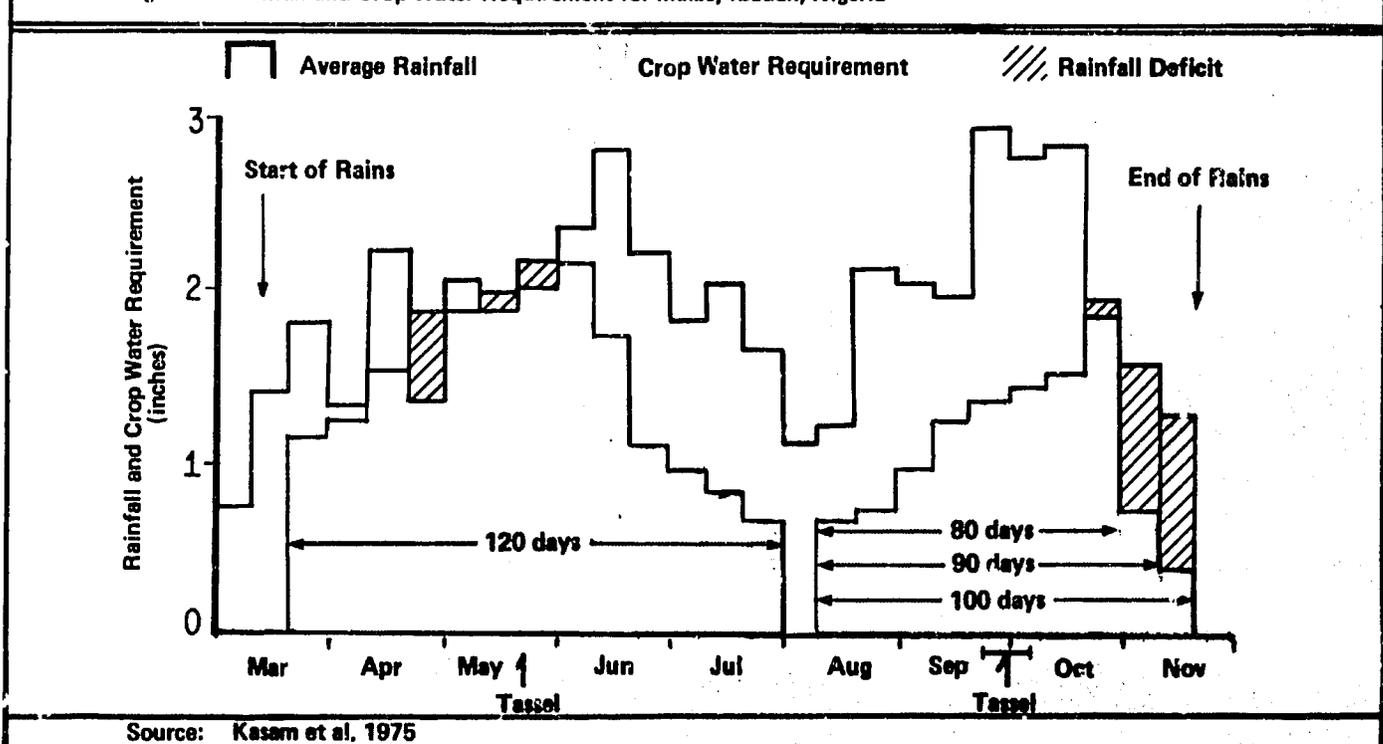
and other inputs. Drought, therefore, is probably responsible for a much higher economic loss than indicated.

Based on greenhouse experiments, field trials and historical analysis of on-farm yield data, agronomists and meteorologists have concluded that drought occurring around flowering has a major effect on grain yield. Deficits of water for periods lasting one to two days during tasseling or pollination may cause as much as 22 percent reduction in yield (Robins and Domingo, 1953), while stress during the grain filling stages (McPherson and Boyer, 1977) and vegetative stages (Denmead and Shaw, 1960) may have much less effect on yield.

It is clear that the most effective means of reducing the effects of drought on maize would be to escape periods of low moisture availability through the manipulation of genotype maturity and planting date. An example of this is given by Kasam *et al.* (1975) for maize grown at Ibadan, Nigeria (Figure 1). At this site total rainfall is about 1,140 mm and is spread from March to November in a bimodal pattern. The first season is long enough for a 120-day maize crop; in the second season, however, crop water requirement can be met without high soil moisture deficits in maize with 80-90 day maturity. Plant breeding programs, therefore, should aim at providing high yielding genotypes with a range of maturities to best fit the season as determined by moisture availability.

Maize grown in large areas of the tropics, however, is affected by drought occurring during and usually in the middle of the main summer growing season. Total rainfall for the crop season may be adequate, but a reduction in the number of days with rain, particularly around the critical

Figure 1. Rainfall and Crop Water Requirement for Maize, Ibadan, Nigeria



Source: Kasam *et al.* 1975

flowering stage of the crop, may have a marked effect on grain yield. The first season at Ibadan illustrates this form of drought. Even though total moisture is adequate, the margin between crop water requirement and water availability is small, particularly in the period just prior to flowering. When water stress occurs at this time, there may be a sizable reduction in grain yield. Mosino and Garcia (1968) suggest that summer drought may affect over 7 million hectares of rainfed maize in Mexico, including most of the lowland tropical area where total rainfall is greater than 1,000 mm. In El Salvador, even though monthly rainfall may average 300 mm, summer drought known as *canicula* may be responsible for reducing yields by 20 percent and is cited as the most frequent source of crop loss as compared to insects, lodging and excess water (Walker, 1980).

Since the exact timing of this drought during the growing season is unpredictable, it cannot be avoided by either genotype maturity or planting date. Furthermore, maize may be the best adapted cereal for these conditions, since high humidity and rain at harvest could be harmful to an alternative crop such as sorghum. To minimize the risk of yield loss, farmers may stagger their plantings of maize, plant maizes of different maturities or intercrop different species. Improved agronomy, such as better weed control and the maintenance of surface mulch (minimum tillage), will have a substantial effect on maize yields under drought. Maize varieties which are better able to resist the effect of reduced moisture, particularly around flowering, also would help stabilize grain yields under these conditions.

This paper therefore examines selection criteria that may be useful in the development of such varieties. It is suggested that for situations where the duration of adequate moisture is limited, yields could be stabilized through the use of genotypes and planting arrangements which escape stress. In situations where moisture availability is predictably inadequate to sustain maize, alternative crop species should be grown or additional moisture provided.

PHYSIOLOGICAL FACTORS AND DROUGHT RESISTANCE

Drought resistance in an agricultural sense refers to the ability of a crop plant to produce its economic product with limited available water. Drought resistance in an evolutionary context, however, would normally be the ability of a plant or species to survive and eventually reproduce under limited moisture. It is likely that the mechanisms responsible solely for survival of a species may in fact differ from those which provide for maximum economic production. The fact that the survival of maize has always relied on the intervention of man, therefore, reduces the probability that this species has evolved strong mechanisms for survival under moisture stress (Qualset, 1979).

Levitt (1972) suggested that the mechanisms for drought resistance (used in the generic sense) be divided into mechanisms of drought escape, drought avoidance and drought tolerance. Drought escape tends to minimize the interacting of drought with crop growth and yield; tolerance gives the ability to produce despite loss of plant water status; avoidance increases the ability to maintain relatively high plant water status despite a shortage of moisture in the environment (O'Toole and Chang, 1979; Fischer and Sanchez, 1979; Fischer and Turner, 1978). However, O'Toole and Chang (1979) note that too often these mechanisms are viewed in terms of either/or (exclusive), implying that a choice is necessary, rather than in terms of and/or (complementary).

Drought escape is often the most important and successful form of drought resistance and is usually imparted through the combination of genotype maturity and planting date. However, due to the unpredictability of the drought being discussed here, drought resistance through escape is generally not feasible and the remainder of this paper concentrates, therefore, on selection for avoidance and/or tolerance mechanisms.

Fischer and Turner (1978) have analyzed plant productivity under arid and semi-arid conditions in terms of total water transpired (obtained), the efficiency with which this water is used (water use efficiency as g dry matter produced per g water transpired), and harvest index (the ratio of economic yield and total dry matter). They found little evidence for consistent cultivar differences in water use efficiency and, thus, yield under moisture-limiting conditions was determined by total transpiration (root exploration, etc.) and harvest index (these two parameters may be antagonistic, i.e. an increase in dry matter partitioned to the root to allow extra root exploration could reduce harvest index of grain). With wheat there is evidence that there is genetic potential to improve both harvest index and root patterns (Fischer and Turner, 1978; Passioura, 1981).

Although the body of information needed to explain the physiological basis for drought resistance continues to grow, it is difficult to discern a major association between a trait (or traits) and drought resistance with application to a breeding program (Fischer and Wood, 1979). One approach used to study the usefulness of a factor for crop improvement is the development of isogenic lines or divergent selections for the character being considered. This approach is time consuming (Moss *et al.* 1974) but may be necessary to unravel the complexity of drought-resistant mechanisms. To determine which factors are more likely to be of consequence, it is useful to compare two species, such as maize and sorghum, which differ markedly in drought resistance but are otherwise adapted to similar environments. In so doing, it must be recognized that the information provided will be as influenced by the

genotype (genotypes) chosen to represent each species as it is by any trait within the species.

A number of studies exist in which maize and sorghum have been compared. Under tropical nonstress conditions in Nigeria, Kassam (1976) measured water use efficiencies of 3.9 and 3.7 mg dry matter/g water for maize and sorghum respectively, while Ludlow (1976) reported values of 2.8 and 3.3 mg/g for the two species respectively. There is no comparable data for stress conditions.

Insofar as the association between particular traits and drought resistance is concerned, Table 1 lists those characters examined by various workers, together with the importance they place on those characters in explaining differences in drought resistance between maize and sorghum. There is not always agreement as to the importance of any one character and this is noted in the table.

Of the traits shown in Table 1, the two that probably are of most importance for the nonprotracted drought are differences in critical water potential (the potential close to zero turgor when stomates close) and differences in developmental plasticity. Neumann *et al.* (1974) measured critical leaf water potentials of -8.1 to -9.6 bars for maize and -11.2 to -13.8 bars for sorghum, while the field data for the two species show values of -16 and -21 bars respectively (Turner, 1974). Thus, sorghum tolerated higher internal water deficits before closing stomata and could continue photosynthesis at lower water potentials (Boyer, 1970a; Beadle *et al.* 1973).

The species also differ in their developmental plasticity. As to sorghum's being more able to avoid the effects of moisture stress at a critical stage of plant development, Whiteman and Wilson (1965) found that inflorescence development could be suspended during stress and resume development after rewatering. Moisture stress, during various stages of panicle development in sorghum, causes a reduction in grain number but, even under severe stress, plants will exert partial panicles (Eastin, 1980). This is in contrast to maize, where stress initially reduces ear size but then reduces the number of ear-bearing plants (increased barrenness). This may be a special feature of the inflorescences of maize—the staminate flowers are produced in the terminal inflorescence and the pistillate flowers on lateral shoots (ears). Further, in sorghum, individual grains have a greater capacity to compensate for a reduction in grain number (Fischer and Wilson, 1975; Fischer and Palmer, 1980). The ability of sorghum to form panicle-bearing tillers makes possible the recovery and grain production of these organs upon relief of water stress.

Understanding the factors controlling ear development and barrenness of plants grown under moisture stress should prove useful to developing drought resistance in maize. Shaw (1977) has estimated the sensitivity of various developmental stages to water stress (Figure 2). The critical period includes flowering and coincides with the time of maximum crop transpiration (Downey, 1971; Andre *et al.* 1978). The pattern of yield reduction due to

Table 1. A Comparison of Sorghum and Maize Traits Associated with Drought Resistance and Estimates of their Relative Importance in Explaining Differences in Productivity under Nonprotracted Moisture Stress

Character	Level of Importance	References
Root Density	High-low	Martin, 1930; Sanchez-Diaz <i>et al.</i> 1969
Root Exploration	Low	Hsiao <i>et al.</i> 1976; O'Toole and Chang, 1979
Root Osmotic Potential	High	Martin <i>et al.</i> 1931; Sullivan and Blum, 1970
Leaf Cuticular Resistance	High-low	Martin, 1930; Yoshida and de los Reyes, 1976
Leaf Stomatal Resistance	Low	Glover, 1959; Boyer, 1970a; Sanchez-Diaz and Kramer, 1971; Beadle <i>et al.</i> 1973
Leaf Size and Rolling	Low	Martin, 1930
Developmental Plasticity	High	Whiteman and Wilson, 1965; Sullivan and Blum, 1970; Eastin, 1980
Critical Potential*	High	Boyer, 1970a; Sanchez-Diaz and Kramer, 1971; Neumann <i>et al.</i> 1974; Turner, 1974; Ludlow, 1976
Osmoregulation	High	Stout and Simpson, 1977; Jones and Turner, 1978; Jurgens <i>et al.</i> 1978; Turner <i>et al.</i> 1978
Desiccation and Heat Tolerance	Low	Sullivan and Blum, 1970

* Water potential at zero turgor

drought stress is similar to the effects of reduced radiation as shown by Fischer and Palmer (1980) and Prine (1971). Tollenaar (1977) recently reviewed the control of grain yield in maize and concluded that the irradiance per plant during flowering was a dominant factor determining grain number. Thus maintenance of photosynthesis during this stage was critical to yield.

In addition to the influence of total dry matter accumulation at the critical period, the partitioning of dry matter to the developing ear and factors affecting spikelet fertility are important in determining grain yield through control of grain number. Fischer and Palmer (1980) reviewed a number of morphophysiological traits that may affect grain number under nonstress conditions; some of these may also be relevant under nonprotracted drought stress.

In tropical maize grown under stress levels of nitrogen, water and density, careful removal of the male inflorescence prior to flowering increased grain yield by 9.5, 21.0 and 17.9 percent respectively (Poey *et al.* 1977). Hybrids with heavier tassels had longer anthesis-to-silking intervals (Daynard, 1968) and lower grain yield under density stress (Buren *et al.* 1974). The drought resistance of a number of hybrids was also related to less leaf area and a shorter interval from mid-anthesis to mid-silking. In the leafier genotypes, leaf development may be at the expense of growth of the developing ear (Dow, 1981).

The interval between anthesis and silking increases under most stress conditions, including drought and high density. This delay in silk development may be related to a decline in nitrate reductase (Hsiao *et al.* 1976), to a reduction in current assimilate supply (Dow, 1981) or to other factors. A number of authors (Jensen, 1971; Duwick, 1977) have advocated selection for reduced interval between

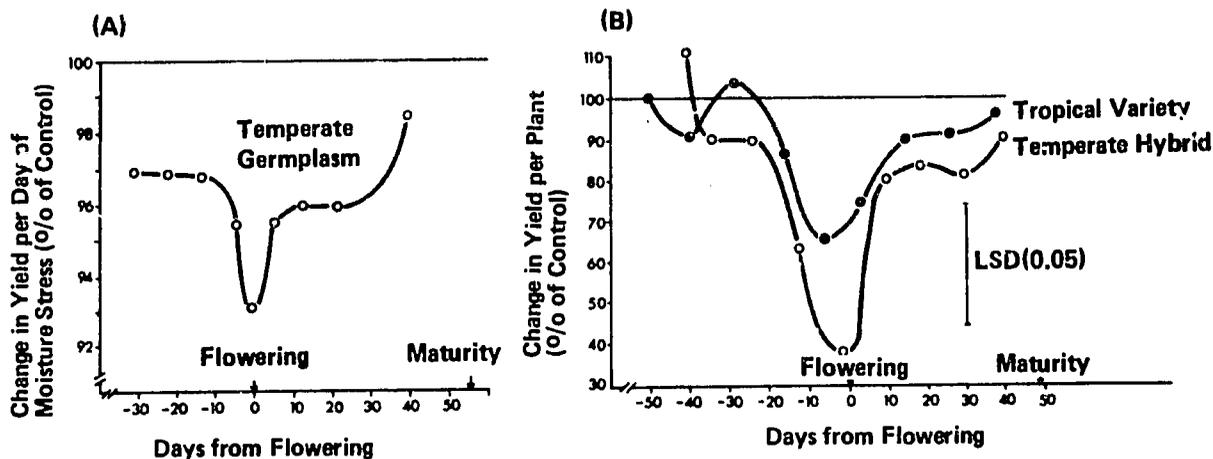
anthesis and silking under population density stress for better performance under moisture stress. Genotypes with a tendency toward prolificacy (two ears) also have better population tolerance (Buren *et al.* 1974). Hallauer and Troyer (1972) reviewed the performance of prolific types and concluded that this character contributes to the reduction of genotype x environment interaction through its ability to adjust to environmental stresses, including drought.

Dow (1981) concluded that hybrids resistant to density stress were also more drought resistant. However, he warned that, while selection for a decrease in the anthesis-to-silking interval under high density, nonmoisture stress conditions would improve drought resistance, other parameters conferring drought resistance could be lost or selected against.

BREEDING FOR IMPROVED DROUGHT RESISTANCE

Blum (1979) has described two major breeding philosophies aimed at improvement of genotypes to stress: "The first and very common approach accepts that a superior yielding variety at the potential level will also yield relatively well under subpotential levels. Drought resistance may be present in such a variety and expressed as an unidentified component of stability in performance over various environments. During the breeding process, yield and stability in performance are handled as one complex. Accumulation of environmentally stable yield genes equates with better performance also under stress situations." This approach has been successful in sorghum (Blum,

Figure 2. Effect on Grain Yield of Maize from a Single Day of Moisture Stress (A) and Eleven Days with 54 Percent Crop Shading (B)



Sources: Shaw, 1977(A) and Fischer and Palmer, 1980 (B)

1979), wheat (Worrall *et al.* 1980) and maize (Russell, 1974; Duvick, 1977). In wheat, improved yield of CIMMYT-derived genotypes over a wide range of conditions is attributed mainly to an increase in yield potential, an increase in environmental stability and a small change in the response of the genotype to environmental conditions (Worrall *et al.* 1980). It appears that some traits, for example improved harvest index of short straw wheats, have a sufficiently strong positive effect on yield under all conditions to give them obvious superiority over traditional varieties or collections, even under dry conditions and despite the specific drought-resistant mechanisms the latter group may possess (Fischer and Wall, 1976). However, subsequent work by Fischer and Wood (1979) did not indicate a relationship between harvest index under irrigated conditions and grain yield under drought.

Gains in maize yields due to breeding in the US Corn Belt from 1930 to 1970 indicate an increase in yield potential; in the more recent commercial hybrids there is considerable improvement at the lower yielding environments (Table 2) (Russell, 1974). The improved performance at the higher stress environments (in this case probably due to moisture availability) might be due to better stalk and root quality brought about by initial selection under high plant density and to the extensive testing of germplasm for yield stability (Russell, 1974).

In view of the lack of sound information on specific drought characters and the considerable scope for

improvement of yield potential, a breeding strategy based on selection under well-watered conditions may very likely be the most efficient (in time) for bringing about rapid progress. This system has the advantage that, under optimal growing conditions, heritabilities for yield are higher than under suboptimal conditions (Johnson and Frey, 1967).

Testing over a large number of sites with varying moisture availability, although expensive, should enable the elimination of those genotypes which may have negative yield traits under moisture stress. Separation of the effects of drought escape and the identification of traits specifically favoring performance under these test conditions could also facilitate selection. For international crop improvement centers such as CIMMYT, testing over a wide geographic range also provides a vehicle for the introduction of improved germplasm into national programs.

"A second approach to breeding for yield performance in a stress environment maintains that indeed potential yield is irrelevant," (Blum, 1979). Varieties must be selected, developed and tested under the relevant conditions. There are a few examples of population improvement in maize based on this procedure. One mass selection study was done in Colombia for the rainy season (600 mm) and dry season (300 mm) separately and in combination (Arboleda-Rivera and Compton, 1974). The selection criterion was grain yield. Three cycles of selection in the rainy season increased yield by 10.5 percent per cycle for that season but increased yield during the dry

Table 2. Changes in Grain Yield since 1930 for Representative US Corn Belt Maize Materials over a Number of Locations

Approximate Year of Release	Maize Type	Grain Yield (t/ha)		Regression Slope
		Mean Across Locations	Maximum	
—	Open-Pollinated	5.48	7.05	1.16
1930	Double-cross Hybrid	5.78	8.03	1.26
1940	Double-cross Hybrid	6.58	8.68	1.01
1950	Double-cross Hybrid	6.75	9.08	1.03
1960	Double-cross Hybrid	7.31	10.15	1.27
1970	Single-cross Hybrid (Public Line)	8.37	10.87	1.06
1970	Single-cross Hybrid (Commercial Line)	8.07	9.30	0.63

Source: Russell, 1974

season by only 0.8 percent. Three cycles of selection during the dry season increased yield by 2.5 percent per cycle in that season and by 7.6 percent in the rainy cycle. Another study in Mexico involved mass selection for a number of cycles under irrigated and/or rainfed conditions (Muñoz, 1975). Testing of the synthetic derived from these selections showed similar performance at the high rainfall, high yielding site, but a greater yield from the selection made under stress at the low rainfall, low yielding site.

An alternative approach to the two strategies described is to improve drought resistance in those materials which already have high yield potential. As improvement in yield potential becomes relatively more difficult to achieve, breeding programs might focus more attention on the identification of specific drought-resistant mechanisms. Finlay and Wilkinson (1963) suggested that, in barley, both yield potential and yield stability over environments could be independently manipulated in a breeding program. In maize, data provided by Russell (1974) clearly demonstrate the importance of improved yield potential in improving yields over a wide range of environments. However, in that work, an analysis of the performance of some of the more recently developed hybrids demonstrated that differences in yield at higher stress environments were due to factors other than yield potential (Table 2).

It is inferred, then, that selection must be for increasing, or at least maintaining, potential yield and, in addition, for improving drought-resistant traits. In maize, it is likely that such traits are multigenic and at a low gene frequency in any given population; their frequency needs to be increased through recurrent selection programs. Increasing the frequency of genes for one or two drought-resistant traits while maintaining yield may lead to an improvement in yield under stress. Recurrent selection for a morphological trait which has a physiological relationship with grain yield has been effective in improving grain yield under nonstress conditions (e.g. Johnson and Fischer, 1979). It is interesting to speculate on the effect on grain yield under stress conditions if a program of recurrent selection for a trait associated with drought resistance is carried out. This would depend on an understanding of drought-resistance mechanisms relative to the ecology for which the material is being developed and on the rapid identification of such mechanisms in large breeding nurseries. At the same time, materials should be evaluated under favorable conditions to maintain or improve yield potential.

Under the influence of natural selection, a few races of maize in various parts of the tropics have developed drought avoidance and/or tolerance mechanisms. One collection, Michoacan 21, was described by Palacios de la Rosa (1959) as having a distinct response to drought and frost; the mechanism was called *latente*. This collection maintained itself under drought without flowering, recovered remarkably on rewatering, was more resistant to permanent wilting at the seedling stage, transpired more than other

lines under irrigation, and transpired less under stress due to stomatal closure (Muñoz, 1975). This response may be due in part to high levels of abscisic acid (Larque-Saavedra and Wain, 1974). The *latente* trait has proven difficult to transfer to higher yielding, agronomically desirable germplasm, particularly in the lowland tropics. However, workers elsewhere have successfully used this material as a source of genes for the improvement of drought resistance in hybrids for the US Corn Belt (Castleberry and Lerette, 1979). In their study, the *latente* trait did not appear to be simply inherited and the development of the drought-resistant hybrids required the selection of inbred lines under controlled moisture conditions for yield and other traits associated with drought resistance.

Many morphological and physiological characters have been suggested for modification so as to enhance either drought avoidance and/or tolerance (Moss *et al.* 1974; Parker, 1968). A number of screening methods have been used to compare the responses of different genotypes of maize to drought and, while some of these methods appear useful in a plant breeding program, there is a paucity of evidence on their use in a population improvement program (Qualset, 1979). In almost all cases cited, the screening of lines was the end product of the breeding program. There are too few reported programs in which selected materials have been recombined and tested. In many cases, also, results obtained in laboratory tests are not further tested under field conditions.

Hurd (1976) has reviewed numerous accounts where plant water stress decreased with increased depth and branching of roots. There may be, however, some ecological conditions where reduced root growth, particularly early in the crop cycle, is an advantage (Passioura, 1972). In maize, Nass and Zuber (1971) measured differences between forty genotypes in terms of total root volume and weight of nodal roots at two growth stages prior to flowering. These characters were correlated with the measured resistance to root pulling of the plants at maturity. Differences in root volume in maize genotypes have also been recorded by Musick *et al.* (1965) and Thompson (1968). Spencer (1940) noted large differences between inbred lines of maize in the rate of development of lateral roots and in the ratio of top-to-root dry weight of seedlings. Muleba (pers. comm.), using young plants grown in solution culture, selected families for superior root weight and length and recombined them to form experimental varieties. Evaluation of these experimental varieties under water stress conditions in the field showed that selection for larger root weight was useful in increasing grain yield under mild water stress while selection for increased root length was superior under severe stress.

The rate of leaf elongation has been shown to be sensitive to changes in leaf water potential (Boyer, 1970b; Watts, 1974) and soil water supply (Acevedo *et al.* 1971). Boyer and McPherson (1975) have suggested that the rate

of cell elongation in seedlings could be used to screen for drought tolerance in cereals. Fischer and Edmeades (1977) used leaf elongation rates to screen maize progenies for drought resistance under field stress conditions.

There has been a considerable breeding effort to modify stomatal response and reduce water loss by transpiration. A number of workers in other crops have been successful in reducing transpiration per unit leaf area (Jones, 1979). Selection has been for the frequency and anatomical structure of the stomata and for measured stomatal conductance (Wilson, 1975). Infrared thermometry has been used to screen large numbers of genotypes for canopy temperature; this can be related to stomatal conductance (Jackson *et al.* 1977; Kretschmer *et al.* 1980).

Williams *et al.* (1967) compared inbreds and hybrids for drought resistance by a) the percentage of seedlings which recovered from a 6-hour exposure to 52°C (heat tolerance), b) germination percentage of seeds exposed to a manitol solution of 15 atmospheres, and c) percentage recovery of seedlings watered 14 days after they had reached wilting. The ratings obtained by each of the three methods were tested by correlation analysis with field evaluations based on the ratio of grain yield under stress to yield under full irrigation. The results suggest that the information from these techniques is correlated with field data and, therefore, any of them would aid a breeding program.

Other workers have used similar techniques. Hunter *et al.* (1936), Tatum (1954), and Kilen and Andrew (1969) showed that the relative differences in response between inbred lines to high temperature coincided with observations of leaf firing in the field. Muñoz (1975) conducted three cycles of mass selection of seedlings which showed good recovery upon rewatering after initially being stressed to the wilting point. Kilen and Andrew (1969) used chlorophyll stability as an index of heat tolerance for inbred lines of maize and found it to be correlated with ratings of leaf firing in the field.

Screening of seeds or seedlings in solutions of different osmotic potential was used by workers as early as 1930 and has had limited results (Ashton, 1948). Parmer and Moore (1968) have modified this technique for maize by the use of polyethylene glycol solutions, and Johnson and Asay (1978) have demonstrated the effectiveness of this osmoticum in differentiating between lines of crested wheatgrass.

Abscisic acid has been shown to be important in drought resistance. In maize, Larque-Saavedra and Wain (1974) measured a large difference of *in vivo*, free abscisic acid between a drought resistant line (Michoacan 21, *latente*) and two European varieties under nonstress and stress conditions. There are no examples of the screening of a larger number of maize genotypes under field conditions for this trait in maize, although such work is being conducted in other cereals (Austin *et al.* 1931).

Recently, screening certain amino acids which increase dramatically under stress has been used as a means of evaluating drought resistance. One of these, proline, was suggested as being useful for drought screening by several workers (Singh *et al.* 1972), but this has been questioned recently (Hanson *et al.* 1977). Results from work with the compound betaine suggest that it may be a valid indicator of the cumulative stress experienced by plants and, if so, discarding genotypes with high betaine content might be effective in selecting for drought avoidance. In maize, Pinter *et al.* (1978) reported that the free asparagine and proline content of plant tissue subjected to drought was positively correlated with drought resistance as estimated from the difference in grain yield under stress and no-stress conditions.

THE CIMMYT EXPERIENCE

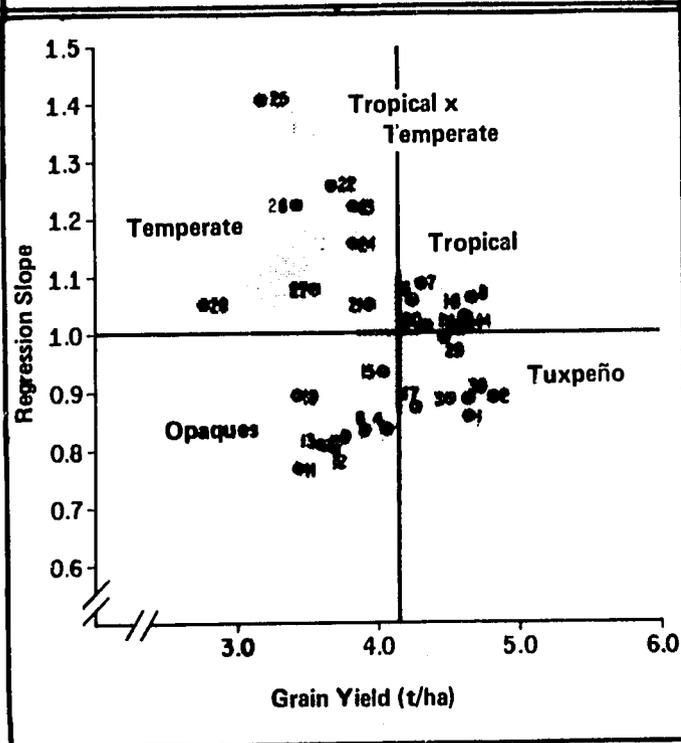
The objectives of CIMMYT's Maize Program are to increase the realized yield and yield potential of a number of adapted maize populations and to improve their yield stability. The breeding and selection system used is described elsewhere (Johnson, 1974, Vasal *et al.* 1978, Paliwal and Sprague, 1981). In 1976, limited work was begun to assess the feasibility of selecting more directly for drought resistance in tropical maize. The objectives were to demonstrate the improvement, through recurrent selection, of the performance of one tropical population exposed to a particular type of drought. In particular, this work was aimed at improving resistance to drought occurring at the critical phase of plant development—flowering. Escape mechanisms would not be utilized.

Choice of Germplasm

Data from the 1973 Experimental Variety Trials (CIMMYT, 1974) were used to identify a population with high and stable yield. Only data from sites which were rainfed were used. Mean yield of each site was significantly correlated with rainfall during the growing season ($r=0.74^*$), suggesting that yield was to some extent influenced by moisture availability. The data were analyzed for yield stability by regression analysis (Finlay and Wilkinson, 1963) and for similarity of response by cluster analysis (Mungomery *et al.* 1974); the results are shown in Figure 3. Within the group of tropical germplasm entries, those with a preponderance of the race Tuxpeño had a slope less than 1.0 and a higher than average mean yield across all sites. The Tuxpeño race has been described by Wellhausen (1956) as one of the most important modern productive races in both the USA and Mexico. Since it is found in areas experiencing limited rainfall during the summer season, it is not unlikely that it may have some natural adaptation to moisture stress. It was therefore decided to use this germplasm as a basis for population improvement for drought.

* Significant at $P = 0.05$

Figure 3. Analysis of Adaptation by Grain Yield and Regression Slope and by Cluster Analysis (Genotypes in Each Shaded Area Having a More Similar Response Than Those Excluded) for an International Experimental Variety Trial Grown only at Rainfed Sites (CIMMYT, 1974)



Development of Suitable Selection Criteria

The emphasis of this work was on field screening. At Tlaltizapan, Morelos, Mexico, there is no appreciable rainfall from October through April; plantings in November are therefore completely dependent on applied water. This site is at 900 m elevation with mean temperatures for the growing season of approximately 28°C maximum and 15°C minimum. The soil is a calcareous vertisol of approximately 1.8 to 2.0 m depth, and overlies a moist, calcareous parent material.

The response of eight maize genotypes (including Tuxpeño-1**) of diverse genetic background to simulated drought conditions at this site was used to develop relevant selection criteria. Irrigation was controlled so that treatments of drought stress commenced from floral initiation and developed through to flowering (to span the critical preflowering-flowering stage), and prior to flowering and continuing through to grain maturity. These treatments reduced grain yield. Fischer and Wood (1979) have defined an index of drought intensity in wheat as one minus the ratio of the mean yield under stress to yield under no stress. Using this index, drought intensities were 0.48 and 0.47 for the stress from floral initiation to flowering and from ten days before flowering to grain maturity respectively. However, although the stress intensity was similar, the yield components affected by the stress differed. In the early stress, grain number was reduced by 45 percent but, because

** Tuxpeño-1 (C₀) represents cycle 11 of recurrent selection for short plants in the population Tuxpeño Crema 1

Table 3. Drought Index Based on Grain Yield of Stress and No-Stress Treatments, and Leaf Water Potential and Stomatal Resistance, Measured at Flowering at Various Times of Day, Subjected to Water Stress from Floral Initiation Onward, Tlaltizapan, 1975

Genotype	Drought Index	Leaf Water Potential (bars)		Stomatal Resistance (sec/cm)	
		0800	1200	0900	1300
Tuxpeño-1	1.43	-2.2	-14.7	5.40	3.60
Pioneer 3369	1.17	-2.1	-14.3	7.41	4.07
Pepitilla	1.09	-2.6	-16.0	7.74	5.25
Mezcla Amarilla	0.75	-3.2	-14.7	8.28	4.83
Super Enanos	0.93	-2.5	-14.6	9.03	4.58
Amarillo del Bajío	0.87	-2.8	-14.7	8.64	4.25
(Mix.1 -Col. C.po.1) -ETO Blanco	0.90	-3.0	-15.3	8.34	4.57
Early Tropical Composite	0.98	-2.1	-17.0	8.57	3.75
LSD*	—	N.S.	-1.7	2.07	0.30

* Significant at 0.05

of the rewatering after flowering, final grain size was not affected. Stress from ten days before flowering through maturity reduced grain number by 33 percent and grain size by 20 percent.

In the work reported here, the response of the eight genotypes to drought was assessed by a drought index based on yield under both fully irrigated and stressed conditions. (The drought index for any one genotype is the ratio of its yield under stress to nonstress, relative to the ratio of the mean yield of all genotypes under stress to nonstress. Thus, a drought index > 1.0 suggests relative drought resistance, and an index < 1.0, relative drought susceptibility.) There were differences between genotypes in both yield potential and drought index; Tuxpeño-1 had both the highest yield potential and drought index score. The ranking of genotypes by drought index was independent of plant height and maturity, measured under nonstress conditions, suggesting that the observed differences in drought index were not due to escape mechanisms. However, yield under nonstress was correlated with drought index ($r = 0.75^*$, unpublished data).

Measurements of leaf water potential and stomatal resistance were made at various stages of crop development and at different times during the day. There were significant differences between genotypes in leaf water potential measured at 1200 hours at flowering (Table 3). However, differences in drought index were correlated ($r = 0.76^*$) with maximum leaf water potential measured at 0600 hours, not with minimum water potential taken at 1200 hours (Table 4). There were significant differences between genotypes in stomatal resistance measured at 0900 and 1300 hours at flowering (Table 3). Stomatal resistance, particularly when measured in the middle of the day, was negatively correlated with drought index (Table 4). Leaf water potential and stomatal resistance also were measured during grain filling in the stress treatment from ten days before flowering to grain maturity. Drought index for this treatment was correlated negatively with stomatal resistance, especially when measured at 1000 hours (Table 4).

The capacity of genotypes to restore maximum water potential during the night (before sunrise) and the ability to maintain open stomata during the day appear to be associated with better performance under the particular stress at this site. While it is suggested that the difference in root morphology may explain some of this differential response, no observations of roots were made.

In this study, two morphological traits--the interval between pollen shed and silking under stress (flower delay) and the rate of stem elongation under stress--were also measured. Stem elongation was positively correlated ($r = 0.84^*$) and the flower delay negatively correlated ($r = -0.66^*$) with drought index. Both traits would appear useful for selection. In subsequent work, a measure of the rate of elongation of a newly exposed leaf was used, rather than

Table 4. Correlation between a Drought Index Based on Grain Yield Under Stress and No Stress and Leaf Water Potential and Stomatal Resistance Measured at Various Times, Taltizapan, 1975

Trait	Time of Measurement		Correlation (r)
Leaf Water Potential	Flowering	0600 hours	0.76*
		1200 hours	0.08
	Grain Filling	0600 hours	0.26
		1200 hours	-0.22
Stomatal Resistance	Flowering	0900 hours	-0.51
		1300 hours	-0.89*
	Grain Filling	1000 hours	-0.72*
		1300 hours	-0.52

Data for eight genotypes
* Significant at 0.05

that of the stem. This measurement was made when the plants in the severe water stress treatment were showing midafternoon leaf rolling; the height from the ground to the youngest visible leaf in the whorl was measured. A week later the measurement was repeated on the same leaf. These measurements were made on six plants per plot in both the irrigated and stress treatments. The extension (which includes components of stem and sheath elongation as well as leaf elongation) under drought was expressed relative to the extension under nonstress so as to free it from genetic differences in elongation rate under no-stress conditions. The relative leaf elongation (RLE) is:

$$RLE = \frac{(HS_7 - HS_0)}{(HI_7 - HI_0)} \times 100$$

Where HI_7 = leaf tip height under irrigation at day 7
 HI_0 = leaf tip height under irrigation at day 0
 HS_7 = leaf tip height under stress at day 7
 HS_0 = leaf tip height under stress at day 0

Differences in leaf area duration were not measured in this study. However, if the supply of assimilates during grain filling is important to performance under drought (as suggested by correlation of drought index and stomatal resistance), then duration of active leaf area also may be an important criterion in explaining genetic differences. In subsequent work, plants were scored visually for leaf tissue death using a scale of 1 to 5 (1--minimum loss, 5--maximum loss). Ratings were made weekly, commencing three weeks after flowering and continuing on a weekly schedule until harvest.

This initial work resulted in the development of a selection index to be used to screen a large number of segregating families. It is based on grain yield under irrigation (yield potential) and drought, flower delay, leaf area loss

during grain fill and relative rate of leaf elongation (RLE). The selection index considers these characters in a multi-spatial arrangement and assigns to them relative distances from a selection target. The distance for each character relative to another can be varied by defining the selected target in terms of standard errors from the mean. Each character is further given a weighting in the overall selection index (Schwarzbach, 1976). Correlations among characters are not taken into account.

An example of the use of this index in selecting the best 10 families (for formation of an experimental variety) and 80 families (for recombination of the next generation) in a progeny trial with 256 entries is given in Table 5. Two additional characters, plant height and maturity under irrigation, are included in the selection. Because of the small plot size used, tall progenies had a competitive advantage for light and therefore had higher yields, particularly under irrigation. Similarly, yield under the stress treatment tended to be positively associated with earlier maturity. The object of the study was to select for drought resistance through mechanisms other than escape. Through the selection index, plant height and maturity are kept constant (relative to the mean of the population) and gains are made for the other characteristics.

The selection target expressed in absolute values and in standard errors from the mean, and the weighting for each of the characters included in the selection index are shown in Table 5. Selection intensity is highest for grain yield under stress and days to flower; it is relatively lower for all of the other characters. For the eighty families

selected for recombination, the selection differentials (mean of selected families minus the population mean) for grain yield under stress and leaf tissue death were approximately one standard error, while those for grain yield under irrigation, flower interval and relative leaf elongation were around 0.5 standard error. The correlations of these characters with grain yield under stress and nonstress conditions are shown in Table 6.

Intrapopulation Variation and Improvement

Using these criteria, eighty-five full-sib families of the population Tuxpeño-1 were screened under moisture regimes similar to those described earlier. A profile of the soil moisture available at flowering and at maturity in the severe stress treatment has been reported elsewhere (CIMMYT, 1981). Analysis of yield indicated a significant genotype x water stress interaction. There was, however, a large increase in the coefficient of variation of the trial under the stress treatment.

Experimental varieties, based on families selected for yield under irrigation and yield under drought, and the divergent selection for resistance and susceptibility based on the selection index, were formed and again grown under similar moisture regimes.

The grain yield of the various experimental varieties under stress and nonstress treatments is shown in Figure 4. There was no significant interaction of variety by water stress level. However, F values for preplanned comparisons among varieties indicate significant varietal differences. When comparing those experimental varieties selected

Table 5. Statistics for Population of 250 Families of Tuxpeño-1, Selection Criteria, and Selections for each of the Characters Used in the Selection for Drought Resistance, Tlaltizapan, 1980

	Grain Yield (kg/ha)		Plant Height (I)	Days to Flower (I)	Flower Intervals (S)	Relative Leaf Elongation (O/O)	Leaf Scores (S)	Canopy Temperature (S) °
	Irrigated (I)	Stress (S)	(cm)	(I)	(days)			(°C)
Population Statistics:								
Mean	5177	1324	175	91.0	5.8	64.6	3.1	28.0
SE	757	428	10.5	2.4	2.3	8.4	0.7	0.8
CV	14.6	32.3	6.0	2.6	40.0	18.0	23.0	2.7
Max.	6865	2918	209	97.6	14.1	93.5	5.0	30.6
Min.	2638	93	141	82.6	.1	44.5	0.9	26.2
Selection Index:								
Target (Absolute)	6691	2608	170	92.2	1.2	77.3	1.7	26.5
Target (Standard Error from Mean)	+ 2.0	+3.0	-0.5	+0.5	-2.0	2.0	-2.0	-2.0
Weighting	2.0	3.0	2.0	3.0	2.0	2.0	2.0	2.0
Selections:								
10 Families	5796	2171	175	91.4	3.2	70.3	2.4	26.8
80 Families	5529	1732	177	91.3	4.4	68.5	2.6	27.1
Differential:** (O/O)	+6.8	+30.8	+1.1	+0.3	-23.4	+11.0	-26.0	-4.0
SE Units	+0.46	+ 0.95	+0.19	+0.13	-0.61	+ 0.45	-1.00	-1.13

* Additional criteria for 1980

** Selection differential for 80 families

Table 6. Coefficient of Linear Correlations (r) between Grain Yields and Other Characters Used for Selecting Drought-Resistant Families in Tuxpeño-1, Grown under Non-stress and Stress Conditions, Tlaltizapan, 1979		
Variable	Grain Yield	
	No Stress	Stress
Grain Yield (Stress)	0.17*	1.00**
Relative Leaf Elongation	-0.15	0.39
Interval between Anthesis and Silking (Stress)	0.04	-0.36**
Leaf Tissue Death (Stress)	-0.15	-0.48**
Canopy Temperature at:		
7 Days before Flowering	—	-0.56**
Flowering	—	-0.73**
Grain Filling	—	-0.65**
Total Dry Matter (No Stress)	0.64**	0.25
Harvest Index (No Stress)	.07	-0.01

* Significant at 0.05
** Significant at 0.01

mainly for grain yield, a significant increase was shown by the variety selected for better grain yield under irrigation when it was grown under no stress. However, under stress conditions there was no significant difference between those varieties, although the experimental variety selected for better grain yield under stress tended toward better grain yield.

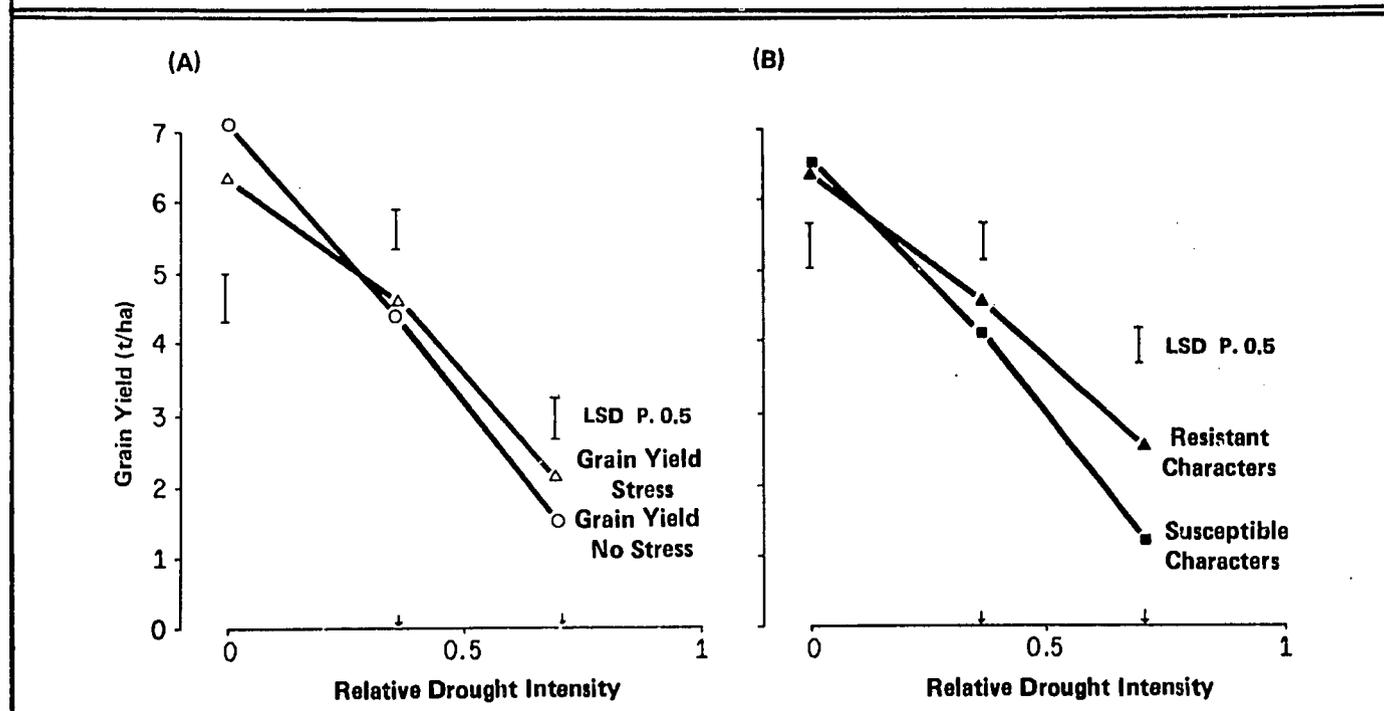
A comparison of the experimental varieties based on the selection index for resistance and susceptibility showed a significant difference under stress; the yield of the resistant and susceptible varieties being 2.3 and 1.5 t/ha respectively. There was, however, no difference in yield under irrigation. Under the stress treatment, the grain yield of the resistant selection was also higher than that of the experimental varieties selected for yield alone.

These studies suggested that a) there is genetic variation within this tropical maize population for performance under these specific drought situations, and b) the inclusion of plant characters in addition to yield enhances the identification of the drought-resistant families.

Based on these findings, a modified recurrent population improvement program was initiated using the Tuxpeño-1 population; it is now in the fourth cycle of selection.

Two hundred fifty-six full-sib families are evaluated at Tlaltizapan, Mexico, during the dry season under two water regimes—normal irrigation and severe stress (no irrigation after planting). Family entries are arranged in a simple lattice (16 x 16) with two replications. For the stress

Figure 4. Influence of Moisture Regime on Performance of Four Experimental Varieties of Tuxpeño-1 when Selected for High Grain Yield under No Stress and Stress (A) and for Physiological Characters for Resistance and Susceptibility to Drought (B), Tlaltizapan, 1976



treatment, there are two such trials (i.e. 4 replications). Plot size is 2 1/2 m in length and 0.75 m wide; plant density is 52,000 plants/ha (2 plants at 50 cm spacing). These families are screened for characters previously discussed and, in addition, to canopy temperature measured with an infrared thermometer (Barnes Instatherm Model 14-220 D-4). Measurements are made in the stress treatment prior to tasseling and between 1100 and 1300 hours. The measurement allows for an approximately 1 meter by 0.40 cm section of canopy of each progeny to be evaluated for mean temperature. The usefulness of this measurement can be seen from the data shown in Table 6. The canopy temperature for 256 families, measured before and at flowering, was negatively correlated with their grain yield ($r = -0.56^*$ and -0.73^* respectively). When used in the selection index, the mean canopy temperature of the 80 families selected for recombination was 1.13 standard error units lower than that of the population mean (Table 5).

Of the 256 families evaluated at the Tlaltizapan site, approximately 80 families are selected, with remnant

seed planted in summer in a crossing block at CIMMYT's lowland tropical station, Poza Rica. A large number of reciprocal full-sib crosses are made at random among the families and, at harvest, 256 ears are saved to constitute the new selection cycle. These families are again evaluated in Tlaltizapan in the winter (dry) cycle.

Evaluation of Progress

An evaluation of progress was conducted after three cycles of recurrent selection for drought resistance in Tuxpeño-1. In addition, there was an evaluation of various cycles of selection for reduced plant height in the population Tuxpeño Crema I, and for reduced tassel (cycle 6), leaf size (cycle 5), and yield and yield stability through the international progeny testing system (Pop. 21, cycle 3), in Tuxpeño-1. The selections for reduced plant height had already been shown to affect maturity and optimum plant density for maximum grain yield. In the evaluation, planting dates for the various cycles of selection for reduced plant height were arranged so that all genotypes in the study

Table 7. Effect on Grain Yield after Selection for Various Characters under Irrigation and Stress Conditions, Tuxpeño Grown at Optimum Density, Tlaltizapan, 1981

Character	Cycle	Grain Yield (kg/ha)		Yield Change/Cycle (% of original)	
		Irrigation	Stress	Irrigation	Stress
Reduced Height ¹	6	5276	1129		
	12	5358	1203	1.0	1.1
	15	5893	1718*	1.3	5.8
	18	6129	1570*	1.3	3.3
Reduced Tassel	0***	5608	1213		
	6	6172	1673*	1.7	6.3
Reduced Leaf	0***	5608	1213		
	5	6196	1468*	2.1	4.1
Drought Resistance	0	5859	1224		
	3	6179	1572*	1.8	9.5
	EV**	6311	1647		
Pop. 21 (Cycle 3) ²	0***	5608	1213		
	3	6458	1315	5.0	2.8
LSD (P=0.05)		899	433		
CV %	11.7	23.8			

* Difference from original cycle significant (preplanned F test) at P=0.05

** Experimental variety (40% selection intensity)

*** Best estimates of original cycle

¹ Planting dates arranged so all cycles flowered at or near ($\pm 1-2$ days) same time

² Selected for yield, stability and wider adaptation through international progeny testing system

flowered at the same date; this served to reduce effects resulting from drought escape mechanisms. The planting density of the cycles of selection for short plants was also varied, based on previous experience, in order to provide an optimum density for each cycle. All of the other selections in the trial were grown at 52,000 plants/ha. There were four replications of each entry in the no-stress treatment and eight replications under stress. Plot size was eight rows of 5 m with a distance of 0.75 m between rows. All harvests were from a well-bordered area of each plot.

The analysis of grain yield under stress and no-stress treatment of various selections grown at their optimum densities is shown in Table 7. The F values for preplanned comparisons show that selection for drought resistance improved grain yield under drought. However, under no stress, there was only a small, nonsignificant increase in grain yield. With 30 percent family selection pressure, the rate of yield increase for the stress conditions was approximately 9.5 percent per cycle. For the experimental variety, representing a 4 percent family selection pressure in the latest improvement cycle (cycle 3), yield under stress was further improved (4.7 percent higher than for cycle 3).

Selection for reduced plant height, tassel size or leaf area resulted in an increase in yield under both water regimes (Table 7). The percentage increase per cycle under moisture stress was 6.3 and 4.1 for tassel and leaf selection,

respectively. Maximum grain yield under stress conditions for the height selections was achieved at cycle 15 with an average gain per cycle of 5.8 percent (from cycles 6 to 15). Further selection for reduced plant height (cycle 18) resulted in a reduction in grain yield under stress but not under the no-stress treatment. The population 21 entry had the highest (5 percent per cycle) yield increase under no stress and a 2.8 percent per cycle increase under stress conditions. For the leaf selection, grain yield per unit leaf area increased from 44.4 to 67.8 g/m² of leaf surface (unpublished data).

Yield was examined in terms of its components--total dry matter and harvest index (Table 8). The selections for drought resistance had a nonsignificant increase (3.0 and 4.5 percent per cycle for cycle 3 and experimental variety respectively) in total dry matter produced under stress. Under irrigated conditions the total dry matter increase was 1.5 percent per cycle for the experimental variety. For the morphological selection for reduced height, tassel and leaf size, there were no significant changes in total dry matter either under irrigation or stress.

Total dry matter can be considered in terms of total water transpired and water use efficiency (g dry matter produced per g water transpired) of the crop. The experiment was not designed to measure these components, but there was an attempt to note differences in rooting density between entries by visually scoring the amount of

Table 8. Total Dry Matter, Harvest Index and Ears Per Plant for Various Selections in Tuxpeño, Grown under Irrigated and Stress Conditions, Tlaltizapan, 1981A

Character	Cycle	Total Dry Matter (kg/ha)		Harvest Index		Ears/100 Plants	
		Irrigated	Stress	Irrigated	Stress	Irrigated	Stress
Reduced Height ¹	6	13653	5408	34.0	15.1	56	
	12	13637	5157	39.1	15.0	65	
	15	12682	5719	42.9	25.6	85	
	18	13043	5327	44.7	25.0	72	
Reduced Tassel	0**	13765	6112	39.5	15.7	58	
	6	14409	6778	41.4	22.2	65	
Reduced Leaf	0**	13765	6112	39.5	15.7	58	
	5	13200	5510	44.3	24.1	73	
Drought Resistance	0	13894	6246	39.6	15.4	57	
	3	14147	6807	38.3	20.9	65	
	EV*	14544	7099	38.2	20.8	74	
Pop. 21 (Cycle 3) ²	0	13765	6112	39.5	15.7	58	
	3	14995	6147	40.3	15.7	56	
LSD (P=0.05)		N.S.	996	6.1	2.0	12.8	
CV %		19.1	15.1	11.6	32.8	16.5	

* Experimental variety (4% family selection)

** Best estimates of original cycle

¹ Planting dates arranged so all cycles flowered at or near (± 2 days) same time

² Selected for yield, stability and wider adaptation through international progeny testing system

root found in soil probe samples taken at 30 cm intervals and a depth of 150 cm (1--low density, 3--high density). This was done at the same time (physiological plant maturity) that volumetric soil moisture measurements were made. There were significant varietal effects in both the root scores and the volumetric moisture content of the soil profile at 120-150 cm (Table 9). Although there were no large differences between entries, there is an indication that both selection for drought resistance and international progeny testing has increased root activity at this depth. The early generation of selection for reduced plant height may have reduced perceived root density at this depth. However, soil moisture was less for the fifteenth cycle for reduced height.

The amount of water used by the crop from the profile 0-150 cm was calculated from measurements of gravimetric moisture and bulk density taken for each entry at germination, flowering and maturity (Table 9). Again there were significant differences, with a tendency for the drought selection, reduced plant height (cycle 15) and the international progeny testing to have increased the amount of water taken up by the crop. Based on these data and those for total dry matter at black layer, an estimate of the

water use efficiency for these materials was made. There does not appear to be a consistent trend with the various selections. The mean value for all selections under stress was 2.5 mg dry matter/g H₂O which is considerably lower than the value of 3.9 mg/g for nonstressed conditions reported by Kassam (1976).

Many of the changes in grain yield are associated with changes in harvest index at optimum plant density (Table 8). For the drought selection, harvest index under drought conditions increased by 9.0 percent per cycle; this appears to be associated with an increase in the number of ear-bearing plants (selection for drought resistance reduced the number of barren plants from 33 to 15 percent). Harvest index increased by 7.7, 6.9 and 10.7 percent for the selection for reduced height (cycles 6 to 15), tassel size and leaf size. For these selections there was also an increase in harvest index under the nonstress conditions (Table 8). However, there may be a limit to the amount of improvement in yield as a result of improved harvest index. Although the harvest index for cycle 18 of the short plant selection was higher under no stress and similar under stress than cycle 15, grain yield and ears per plants under stress were lower. In the drought selections, the higher yield of the

Table 9. Visual Estimate of Root Activity, Soil Moisture Content, Water Use and Estimated Water Use Efficiency for Various Selections of Tuxpeño, Grown under Stress Conditions

Character	Cycle	Root Density Score * (120-150 cm)	Soil Moisture Content (120-150 cm) (o/o)	Water Use to Black Layer (mm)	Estimated Water Use Efficiency (mg dry matter/g H ₂ O)
Reduced Height ¹	6	2.02	41.7	206	2.62
	12	0.96	41.6	210	2.45
	15	1.21	31.0	286	1.99
	18	0.84	41.0	245	2.17
Reduced Tassel	0 **	0.96	42.1	217	2.81
	6	1.12	41.6	231	2.93
Reduced Leaf	0 **	0.96	42.1	217	2.81
	5	0.87	41.2	235	2.34
Drought Resistance	0	0.84	42.7	228	2.74
	3	1.28	35.2	275	2.47
	EV ***	1.27	38.6	257	2.76
Pop. 21 (Cycle 3) ²	0	0.96	42.1	217	2.81
	3	1.37	39.5	261	2.35
LSD (P=0.05)		0.5	5.4	6	—
CV %		30	26	23	—

* Score (1--low, 3--high)
 ** Best estimate of original cycle
 *** Experimental variety (40/o family selection)
 1 Planting dates arranged so all cycles flowered at or near ($\pm 1-2$ days) same time
 2 Selected for yield, stability and wide adaptation through international progeny testing system

experimental variety under stress was associated not with a higher harvest index but with a tendency for greater total dry matter and more ears per 100 plants.

Data in Table 10 show the relationships between a number of characters which may influence the number of ear-bearing plants (and hence harvest index) and grain yield under stress. The variation in each character is that which exists between the various selections of Tuxpeño included in the trial. Although not all of the correlations are

significant ($n=10$), the trends in the relationship are similar to those found for the variation between families indicated earlier. Thus, grain yield under stress is correlated with flower interval (-0.71^*), relative leaf elongation (0.65^*) and canopy temperature (-0.35^*) measured under stress. Tassel and stem dry weight and leaf area index, measured under irrigated conditions, also were correlated with grain yield under stress. Correlation values (r) were -0.58 , -0.51 and -0.64^* respectively.

Table 10. Statistics for Characters Associated with Grain Yield Production under Stress (Drought Resistance) for Selections within the Population Tuxpeño-1, Tlaltizapan, 1981A

Parameter	Dry Matter at Flowering (kg/ha)**			Leaf Area Index **	Relative Leaf Elongation (%)	Flower Delay (days)	Canopy Temperature (°C)
	Total	Stem	Tassel				
Mean	13845	4105	504	3.44	59.5	5.3	33.3
Maximum	14995	5339	650	4.15	71.8	9.2	35.0
Minimum	12682	3682	386	2.82	50.8	3.7	31.6
F Ratio	11.7**	4.3**	8.3**	22.1**	7.82**	10.8**	5.5**
CV %	19.0	15.3	15.2	5.8	10.4	21.7	5.3
Correlation with Grain Yield under Stress (n = 10)	0.29	-0.51	-0.58	-0.64**	0.65**	-0.71*	-0.35

* Significant at 0.05
** No-stress conditions

CONCLUSIONS

This study shows that there is an opportunity to select within the population Tuxpeño-1 for improved yield under stress (drought resistance), while maintaining its relatively high yield potential. While the findings are for only one population exposed experimentally to a specific type of drought, the procedures used are applicable to other maize populations and localities.

Improvement in drought resistance is much more rapid when the selection procedure uses more characters than just grain yield *per se*; many factors are involved in conferring drought resistance. The use of a selection index based on relative leaf elongation, the interval between pollen shed and silking, canopy temperature, leaf area loss, and grain yield under stress and no stress resulted in maximum gain per cycle in grain yield under stress (9.5 percent).

Selection for drought resistance requires a field site with uniform and controlled moisture and sufficient area for adequate replication of progenies. All of the criteria used can be measured rapidly and are therefore suitable for screening a large number of progeny and, with the exception of canopy temperature, require no sophisticated instrumentation. Relative leaf elongation, canopy temperature and the interval between pollen shed and silking can all be measured prior to pollination and, when combined, account for 54 percent ($R^2 = 0.54^*$) of the variation in grain yield under stress conditions.

Morphological selection for reduced height, tassel size and leaf size, made under nonstress conditions,

also improved grain yield under stress. These criteria are easily incorporated into a breeding program and can be used for individual plant selection. Tuxpeño-1 (Pop. 21), improved for general agronomic characters and wide adaptability through the International Progeny Testing System, showed high gain per cycle in grain yield under nonstress conditions and also improvement in yield under stress conditions (although gain per cycle was lower).

In all of the selections studied, most of the yield improvement was a result of those processes which reduced barrenness and increased harvest index. There was, however, some indication that the selection index also changed the rooting pattern and enhanced total dry matter production. Since all of the selection criteria may alter components of drought resistance, there appears to be a need to incorporate all characters into the selection process. An ideal breeding program would simultaneously evaluate progeny for criteria used in the selection index and make use of within-family (individual plant selection) variation for the desirable morphological traits during the recombination cycle.

Significant gains in yield under stress conditions were achieved after only three cycles of recurrent selection. Continuing the selection and accumulation of genes for drought resistance traits, while at the same time maintaining yield potential, should lead to further improvement in yield under stress. There should be ample variation for these traits within the already available productive and well-adapted tropical germplasm.

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17

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18

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