

PHYSIOLOGICAL RESPONSES OF THREE
MAIZE (Zea mays L.) POPULATIONS TO
SELECTION FOR HIGH GRAIN YIELDS

by

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RAPID ESTIMATION OF LEAF AREA AND YIELD EFFICIENCY
IN MAIZE (ZEA MAYS L.) POPULATIONS

Grain yield of maize plants can be increased by increasing light utilization efficiency of leaf surfaces. The leaf area index (LAI) at which agronomic experiments are conducted is measured to determine the possibilities of further yield increase. Grain yield efficiency (grain yield per unit of leaf area) appears to be associated with density tolerance (1, 6). To select for this criterion, plant leaf area (LAp) as well as grain yield must be measured. Present methods of estimating leaf area, whether electronic or as outlined by Montgomery (4) and McKee (3), are expensive or time consuming and have limited utilization to plant scientists working with large plant numbers.

Rapid methods of estimating leaf area of maize plants in replicated trials have been proposed by Francis, Rutger and Palmer (2) and Pearce, Mock, and Bailey (5). They used narrow genetic-based genotypes (inbred lines and single cross hybrids) in temperate environments. Rapid methods of estimating leaf area have not been developed for tropical environments or for broad genetic-based populations. The concern of a plant breeder in screening genotypes for yield efficiency is not the actual leaf area (LA) of each genotype, but the magnitude of genetic variation in yield efficiency within the materials under selection. A system that could directly or indirectly provide rapidly such information at low cost would be useful.

Present studies were established to test methods of rapidly estimating LA developed for narrow-based genotypes under temperate

conditions (2, 5) for use with broad genetic-based populations under tropical conditions, and to devise a rapid method of estimating variation in grain yield efficiency.

MATERIALS AND METHODS

Three broad genetic-based maize populations, Mex-Mix, Kansas Drought Synthetic (KDS), and Amarillo Bajio, were used. Mex-Mix is a composite derived from a mixture of 1000 temperate and tropical varieties. It was subjected to mild selection pressure for yield efficiency after one generation of random mating. Its general agronomic responses are typical of tropical germplasm, although it has some temperate material in its background. KDS is a temperate synthetic population developed by intercrossing inbred lines selected for performance in hybrid combination under drought conditions. Amarillo Bajio is a CIMMYT (International Maize and Wheat Improvement Center) population. It is a semi-temperate open-pollinated population developed in Mexico from Caribbean and some U.S.A. cornbelt germplasm.

One-hundred half-sib families generated in each population were grown simultaneously at Tlaltizapan, Morelos, Mexico, and at Manhattan, Kansas, during summer 1974. The field design at the two locations was a randomized block with two replications. At Tlaltizapan, each half-sib family was grown in 4-row plots 5 m long with 0.75 m between rows and 0.25 m between plants (53,333 plants/ha). Plots at Manhattan consisted of two 5-m rows. Spacings between rows and between plants in each row were 0.75 m and 0.24 m, respectively (55,555 plants/ha). Plots were fertilized and irrigated for maximum grain production.

Total plant leaf area (LAp) at anthesis was measured according to Montgomery (4) in all replications at Tlaltizapan and in the first replication at Manhattan. Area of each leaf position on a single plant was estimated from four plants in each plot. The LAp was computed by summing the LA of all the leaf positions on a single plant. Leaf positions were determined from the top (flag leaf = no. 1) downward. Correlation studies and multiple regression analyses were conducted with Tlaltizapan data to determine the relationship between the LAp and the LA of each leaf position, and the combinations of LA of two or three leaf positions that best predict LAp.

A total of 8 "LA factors" were computed in the first replication according to Francis et al. (2), but with some modifications. Those included dividing LAp by the LA of leaf 7, 8, and 9 or the sum of LA of leaves 2+9, 2+11, 7+11, 7+11+2, and 11+9+2. Estimations of LAp in the second replication were done by multiplying the LA of leaves 7, 8, and 9, and the sum of LA of leaves 2+9, 2+11, 7+11, 7+11+2 and 11+9+2, in this replication by their respective "LA factor" computed in the first replication. Correlation studies were run with data from each family in each population to determine the degree of association between the observed LAp and each estimated LAp.

At Manhattan, ears were harvested from the first ten plants bordered by other plants at maturity. Grain was dried by forced air to a constant weight at 70C, shelled from the ears and weighed. The plant yield efficiency (YEp) was computed by dividing the kernel weight per plant (YP) by the LAp for each plot. Eight leaf yield efficiencies (YE_L) values were calculated by dividing the YP respectively by the LA

of leaves 7, 8, 9, 2+9, 2+11, 7+11, 7+11+2 and 11+9+2. Correlation studies were conducted to determine the degree of association between YEp and each of the leaf yield efficiencies (YE_L) that could be used as rapid methods for screening genotypes for yield efficiency.

RESULTS AND DISCUSSION

Average LA of the first thirteen individual leaves, beginning with the flag leaf, and their correlation with LAP are presented in Tables 1 and 2, respectively. All correlation values are highly significant. The highest correlation occurred with leaf 8 in KDS, leaf 9 in Amarillo Bajio, and leaf 7 in Mex-Mix.

Though leaf 7 was the largest or nearly the largest in these populations, the area of the leaf with the highest correlation coefficient with LAP was not always the largest leaf on the plant as reported by Francis et al. (2). Consequently, multiple regression analyses were conducted to determine the combinations of two or three leaf positions whose area best predicted LAP (Table 3). Eight "LA factors", computed for the first replication from leaf 7, 8 and 9, and the combination of two or three leaf positions (2+9, 2+11, 7+11, 7+11+2, and 11+9+2) that best predicted the LAP in at least two populations were used to estimate LAP in the second replication.

Table 4 shows the observed population mean of total plant leaf area (\overline{LAp}) in the second replication, the estimated \overline{LAp} in the same replication from different "LA factors" estimated in the first replication, and the correlation coefficient between these two values. A t-test comparing the observed \overline{LAp} and each estimated \overline{LAp} did not show

Table 1. Average area of individual leaves and total plant leaf area of three maize populations at Tlaltizapan, Mexico, during 1974

| Leaf position | KDS | | Amarillo Baj. | | Mex-Mix | |
|---------------|----------------------------|----------|---------------|----------|---------|----------|
| | Mean | σ | Mean | σ | Mean | σ |
| | -----dm ² ----- | | | | | |
| 1 | 1.74 | 0.31 | 2.10 | 0.40 | 2.04 | 0.52 |
| 2 | 3.39 | 0.42 | 4.12 | 0.51 | 3.79 | 0.75 |
| 3 | 4.54 | 0.48 | 5.68 | 0.60 | 5.19 | 0.91 |
| 4 | 5.36 | 0.49 | 6.76 | 0.51 | 6.16 | 1.03 |
| 5 | 5.87 | 0.54 | 7.48 | 0.56 | 6.86 | 1.13 |
| 6 | 6.13 | 0.56 | 7.87 | 0.51 | 7.31 | 1.20 |
| 7 | 6.02 | 0.61 | 7.88 | 0.54 | 7.31 | 1.23 |
| 8 | 5.55 | 0.73 | 7.42 | 0.59 | 6.87 | 1.25 |
| 9 | 4.67 | 0.73 | 6.52 | 0.69 | 6.09 | 1.30 |
| 10 | 3.72 | 0.93 | 5.32 | 0.71 | 4.94 | 1.16 |
| 11 | 2.67 | 0.65 | 4.08 | 0.68 | 3.87 | 1.09 |
| 12 | 1.65 | 0.70 | 2.91 | 0.62 | 2.70 | 0.90 |
| 13 | 0.74 | 0.53 | 1.74 | 0.60 | 1.68 | 0.80 |
| Total | 52.34 | 6.33 | 71.21 | 6.22 | 64.67 | 11.02 |

Table 2. Correlation of area of individual leaves with total plant leaf area of three maize populations at Tlaltizapan, Mexico, during 1974

| Leaf position | KDS | Amarillo Bajio | Mex-Mix |
|---------------|-------------|----------------|---------|
| | -----r----- | | |
| 1 | 0.463** | 0.355** | 0.494** |
| 2 | 0.473** | 0.435** | 0.596** |
| 3 | 0.638** | 0.410** | 0.674** |
| 4 | 0.791** | 0.572** | 0.700** |
| 5 | 0.809** | 0.649** | 0.705** |
| 6 | 0.865** | 0.752** | 0.718** |
| 7 | 0.921** | 0.824** | 0.723** |
| 8 | 0.936** | 0.812** | 0.680** |
| 9 | 0.917** | 0.842** | 0.563** |
| 10 | 0.786** | 0.792** | 0.569** |
| 11 | 0.855** | 0.775** | 0.461** |
| 12 | 0.687** | 0.723** | 0.421** |
| 13 | 0.707** | 0.639** | 0.360** |

** = r significant at $P = 0.01$ level.

Table 3. Combinations of two and three leaf positions that best predict total plant leaf area of three maize populations at Tlaltizapan, Mexico, during 1974

| KDS | | | Amarillo Bajio | | | Mex-Mix | | | | | |
|--------|----------------|---------|----------------|--------|----------------|----------|----------------|--------|----------------|-------|-------|
| 2-leaf | | 3-leaf | 2-leaf | | 3-leaf | 2-leaf | | 3-leaf | | | |
| Leaves | R ² | Leaves | R ² | Leaves | R ² | Leaves | R ² | Leaves | R ² | | |
| 4+11 | 0.953 | 7+ 2+11 | 0.970 | 9+ 2 | 0.826 | 9+13+ 2 | 0.840 | 3+ 7 | 0.539 | 7+3+2 | 0.546 |
| 9+ 4 | 0.943 | 4+ 8+11 | 0.968 | 9+ 4 | 0.809 | 9+ 2+14 | 0.839 | 4+ 7 | 0.538 | --- | --- |
| 3+11 | 0.941 | 4+14+ 9 | 0.968 | 2+10 | 0.803 | 11+ 9+ 2 | 0.838 | 5+ 7 | 0.532 | --- | --- |
| 5+11 | 0.935 | 4+ 9+13 | 0.968 | 9+ 3 | 0.802 | 9+ 2+ 5 | 0.837 | 8+ 4 | 0.532 | --- | --- |
| 2+11 | 0.933 | 4+ 9+11 | 0.967 | 9+ 1 | 0.801 | 11+ 6+ 2 | 0.835 | 7+11 | 0.53 | --- | --- |
| 5+ 9 | 0.932 | 4+ 6+11 | 0.966 | 9+ 5 | 0.796 | 7+ 2+11 | 0.834 | 8+ 3 | 0.529 | --- | --- |
| 6+11 | 0.931 | 7+ 3+11 | 0.966 | 6+11 | 0.796 | 9+10+ 2 | 0.833 | 12+ 7 | 0.529 | --- | --- |
| 6+ 9 | 0.927 | 4+10+11 | 0.966 | 7+11 | 0.788 | 7+10+ 2 | 0.832 | 9+ 7 | 0.528 | --- | --- |
| 4+ 8 | 0.927 | 3+14+ 9 | 0.965 | 4+10 | 0.787 | 12+ 9+ 2 | 0.831 | 6+ 7 | 0.528 | --- | --- |
| 3+ 9 | 0.925 | 2+ 6+11 | 0.965 | 2+11 | 0.781 | 9+ 6+ 2 | 0.830 | 7+10 | 0.528 | --- | --- |

R² = multiple regression coefficient.

Table 4. Estimated total plant leaf area in second replication using leaf area factors calculated from different leaf combinations in the first replication and correlation coefficients between estimated and observed total plant leaf areas of three maize populations at Tlaltizapan, Mexico, during 1974

| Leaf position | KDS | | | | Amarillo-Bajio | | | | Mex-Mix | | | | | | |
|---------------|----------------------------|---------|-----------|---------|----------------------------|---------|-----------|---------|----------------------------|---------|-----------|---------|-------|-------|---------|
| | Observed | | Estimated | | Observed | | Estimated | | Observed | | Estimated | | | | |
| | Mean | St.dev. | Mean | St.dev. | Mean | St.dev. | Mean | St.dev. | Mean | St.dev. | Mean | St.dev. | | | |
| | r | | | | r | | | | r | | | | | | |
| | -----dm ² ----- | | | | -----dm ² ----- | | | | -----dm ² ----- | | | | | | |
| 7 | 51.80 | 7.92 | 52.40 | 7.46 | 0.787** | 71.31 | 8.62 | 71.97 | 9.93 | 0.586** | 67.99 | 9.77 | 68.33 | 9.29 | 0.743** |
| 8 | 51.80 | 7.92 | 52.16 | 8.49 | 0.844** | 71.31 | 8.62 | 72.44 | 9.75 | 0.748** | 67.99 | 9.77 | 67.25 | 9.37 | 0.844** |
| 9 | 51.80 | 7.92 | 52.27 | 9.38 | 0.835** | 71.31 | 8.62 | 71.59 | 9.85 | 0.767** | 67.99 | 9.77 | 68.31 | 10.67 | 0.864** |
| 2+ 9 | 51.80 | 7.92 | 52.60 | 8.75 | 0.899** | 71.31 | 8.62 | 72.07 | 9.81 | 0.761** | 67.99 | 9.77 | 68.89 | 10.94 | 0.849** |
| 2+11 | 51.80 | 7.92 | 53.29 | 14.28 | 0.707** | 71.31 | 8.62 | 72.86 | 12.06 | 0.831** | 67.99 | 9.77 | 70.22 | 13.10 | 0.870** |
| 7+11 | 51.80 | 7.92 | 52.48 | 9.72 | 0.815** | 71.31 | 8.62 | 71.97 | 9.51 | 0.840** | 67.99 | 9.77 | 68.72 | 9.89 | 0.932** |
| 7+11+2 | 51.80 | 7.92 | 52.67 | 9.20 | 0.860** | 71.31 | 8.62 | 72.19 | 9.34 | 0.841** | 67.99 | 9.77 | 69.01 | 9.92 | 0.930** |
| 11+ 9+2 | 51.80 | 7.92 | 52.64 | 10.17 | 0.879** | 71.31 | 8.62 | 72.13 | 10.21 | 0.860** | 67.99 | 9.77 | 69.10 | 11.20 | 0.928** |

** = r significant at 0.01 probability level.

any significant difference. This indicates that the same population mean was estimated. All correlation coefficients between the two values were highly significant. The highest correlation coefficient was observed with the sum of LA of leaves 2+9 in KDS, 2+9+11 in Amarillo Bajio, and 7+11 in Mex-Mix.

When the "LA factor" was computed on a single leaf basis, the highest correlation coefficient was with the leaf position whose area was most correlated with LAp. However, this may not always be true in highly heterogeneous populations, such as Mex-Mix, where it may occur with other leaf positions.

The "LA factor" computed on the basis of the sum of areas of two or three leaf positions usually improved the correlation between the observed and estimated LAp obtained from single leaves. But, this difference is of relatively little interest, since a good estimation of LAp can be obtained with almost the same accuracy and less labor using a single leaf.

The experiment did not show any advantage of leaf 7 over leaf 8 or leaf 9 in the estimation of LAp in the second replication. Instead, the magnitude of the correlation between the observed LAp with the estimated LAp, using the "LA factor" calculated with leaf 7, tended to be relatively lower than that of either leaf 8 or leaf 9 in all three populations. Leaf 8 or leaf 9 may indiscriminately be used in the computation of the "LA factor" whether for tall populations with a large canopy, as Mex-Mix, or short populations with a small canopy, as KDS.

Table 5 shows plant yield efficiency (YE_p) (grain yield per unit of total leaf area at silking), leaf yield efficiencies (YE_L)

Table 5. Correlation and variation of total plant yield efficiency (YE_p) (grain yield per unit total plant leaf area) with leaf yield efficiency (YE_L) (grain yield per unit of individual or sum of individual leaf areas) of three maize populations in the first replication at Manhattan during 1974

| Leaf position | KDS | | | | | | Amarillo Bajio | | | | | | Mex-Mix | | | | | |
|---------------|-------------------|----|-------|-------------------|---------|--|-------------------|----|-------|-------------------|---------|--|-------------------|----|-------|-------------------|---------|--|
| | YE _p | | | YE _L | | | YE _p | | | YE _L | | | YE _p | | | YE _L | | |
| | Mean | CV | | Mean | CV | | Mean | CV | | Mean | CV | | Mean | CV | | Mean | CV | |
| | g/dm ² | % | | g/dm ² | % | | g/dm ² | % | | g/dm ² | % | | g/dm ² | % | | g/dm ² | % | |
| 7 | 1.67 | 19 | 17.14 | 19 | 0.912** | | 1.17 | 22 | 14.12 | 24 | 0.885** | | 0.96 | 30 | 10.90 | 28 | 0.954** | |
| 8 | 1.67 | 19 | 16.79 | 18 | 0.924** | | 1.17 | 22 | 13.31 | 23 | 0.888** | | 0.96 | 30 | 10.47 | 30 | 0.940** | |
| 9 | 1.67 | 19 | 16.96 | 19 | 0.954** | | 1.17 | 22 | 13.07 | 22 | 0.911** | | 0.96 | 30 | 10.89 | 29 | 0.972** | |
| 2+9 | 1.67 | 19 | 12.69 | 18 | 0.938** | | 1.17 | 22 | 9.69 | 22 | 0.900** | | 0.96 | 30 | 7.71 | 30 | 0.958** | |
| 2+11 | 1.67 | 19 | 14.05 | 20 | 0.965** | | 1.17 | 22 | 10.12 | 22 | 0.928** | | 0.96 | 30 | 8.37 | 30 | 0.966** | |
| 7+11 | 1.67 | 19 | 9.10 | 19 | 0.972** | | 1.17 | 22 | 6.97 | 22 | 0.956** | | 0.96 | 30 | 5.76 | 29 | 0.970** | |
| 7+11+2 | 1.67 | 19 | 7.71 | 19 | 0.970** | | 1.17 | 22 | 5.88 | 22 | 0.936** | | 0.96 | 30 | 4.73 | 29 | 0.969** | |
| 11+9+2 | 1.67 | 19 | 7.68 | 19 | 0.976** | | 1.17 | 22 | 5.68 | 22 | 0.952** | | 0.96 | 30 | 4.72 | 29 | 0.976** | |

** = r significant at 0.01 probability level.

(grain yield per unit of leaf area) of leaves 7, 8, 9, 2+9, 2+11, 7+11, 7+11+2, and 11+9+2, coefficient of variation for each of the observed means, correlation coefficient of YE_p and each of YE_L . All the leaf yield efficiencies varied closely and highly significantly with plant yield efficiency. The coefficient of variation remained almost constant in each population regardless of the method used to calculate yield efficiency. Yield efficiency of different families in a population can be differentiated by any of the methods used in this experiment.

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RELATIONSHIP OF PHYSIOLOGICAL SELECTION CRITERIA TO GRAIN
YIELD OF MAIZE (ZEA MAYS L.) POPULATIONS

The increasing world food shortage is challenging plant breeders and agronomists to produce higher cereal grain yields. The maximum grain yield that can be obtained with a given crop determines the potential for increased yield. Twenty-seven tons/ha were estimated (7) as the maximum grain yield that can be obtained with a highly photosynthetically efficient maize plant translocating 770 kg/ha/day of dry matter to the growing kernels during a grain filling period of 35 days. The highest maize grain yield ever observed, 19 tons/ha, was under irrigation in Colorado in 1969 (4). Investigations are still needed to move the actual maize grain yield levels towards their upper limits.

Grain yield of cereal crops has been partitioned into components and summarized (8) in a formula:

$$\frac{\text{grain yield}}{\text{land area}} = \frac{\text{Plant number}}{\text{land area}} \times \frac{\text{ear number}}{\text{plant number}} \times \frac{\text{kernel weight.}}{\text{ear number}}$$

Kernel weight is equal to 1000 kernel weight $\times \frac{\text{kernel number}}{\text{ear number}}$. This provides plant breeders and agronomists with a better understanding of components they may manipulate to increase grain yields. Most contemporary maize cultivars, developed mainly on the basis of yield per plant, react to increased planting densities by increased barrenness and lodging (1, 17, 19). Also, except for data from Pendleton et al. (15), increasing photosynthetic efficiency by using upright leaf cultivars failed to yield higher kernel weights at densities above 40,000 plants/ha (16, 18).

Some maize traits associated with density tolerance have been reported: high grain weight per unit leaf area or yield efficiency (3, 17), shorter pollen shed-to-silking interval, prolificacy, and smaller tassel size (3). Short plants with small leaf area and early maturation have also been reported to be density responsive, although they did not outyield tall plants with larger leaf area within the range of experimental population densities (9, 21).

The potential grain yield of a maize plant is determined by the number of grains (sink capacity) established at anthesis and by the amount of assimilates available to the developing kernels. Thus, a sensible approach to increasing grain yield must be based on the interaction between photosynthetic source (leaves) and storage capacity during grain filling. Experiments were conducted to study the relationships of some leaf characteristics associated with photosynthesis rate during grain filling with grain yield, yield efficiency, and yield components in three open-pollinated maize populations.

MATERIALS AND METHODS

Experiment I

Three maize populations, Mex-Mix, Kansas Drought Synthetic (KDS), and Amarillo-Bajio, were used. Mex-Mix is a wide-based population derived from a mixture of over 1000 temperate and tropical varieties. It was subjected to mild selection pressure for yield efficiency after one generation of random mating. KDS is a synthetic population developed by the Kansas Agr. Exp. Sta. by intercrossing inbred lines selected for their performance in hybrid combinations under drought conditions.

Amarillo-Bajio is a semi-temperate open pollinated population developed from Caribbean and some U.S. cornbelt germplasm in Mexico.

One-hundred half-sib families were generated in each population at Tlaltizapan, Morelos, Mexico, during October 1973 to April 1974. The families were evaluated in yield trials at Tlaltizapan, Mexico, and Manhattan, Kansas, during summer 1974.

The experimental design at both locations was a randomized block with two replications. At Manhattan, each half-sib family was grown in 2-row plots 5 m long with 0.75 m between rows and 0.24 m between plants (55,555 plants per ha). Two-hundred kg/ha of N as ammonium nitrate was applied to the soil prior to planting. The soil was high in K and P content. The field was routinely irrigated after the silking stage of maize. Some damage to leaves occurred during a storm August 17, 1974. Grain yield was determined by harvesting ears from the first ten plants bordered by other plants during mid-October 1974. Grain was dried by forced air to constant weight (11% moisture) at 70 C, shelled from the ears, and weighed.

Plots at Tlaltizapan consisted of four 5-m rows. Spacing between rows and between plants in each row were 0.75 m and 0.25 m, respectively (53,333 plants/ha). Planting and irrigation were similar to that at Manhattan. One-hundred kg per ha of N as ammonium sulfate and 44 kg per ha of P as superphosphate were applied prior to planting; 150 kg N/ha was top-dressed in equal applications at the 7 to 9-leaf stage and immediately before tasseling.

The Tlaltizapan soil was newly leveled for irrigation. Leveling exposed an alkaline subsoil that was imbalanced nutritionally (available P, 7/kg/ha; exchangeable K, 670 kg/ha; available Mg, 684 ppm; available Ca,

4702 ppm; available Zn, 0.59 ppm; available Fe, 7.79 ppm; and pH, 7.6). Some families in each population developed severe symptoms resembling Mg deficiency. These were rated using a 1 to 5 scale (1 = all leaves showing normal color and 5 = severe chlorosis in all leaves). Ears were harvested from all plants in the two center rows, except for the end plants in each row, in mid-November. The number of harvested plants (PN) in each plot was recorded. Grain yield per plant (YP) was adjusted to 15% grain moisture percentage.

Flowering date (FD) was the number of days from planting to 50% silking. Leaf area index (LAI) and specific leaf weight (SLW) were measured shortly after anthesis at both locations. The LAI was estimated as the product of plant density and average leaf area per plant calculated as leaf length x width x 0.75 (12). Leaf area of the first four bordered plants in each plot was measured at Tlaltizapan. At Manhattan, the leaf area in the second replication was estimated by multiplying the average leaf area of the 7th (KDS), 9th (Mex-Mix), and ear leaf (Amarillo-Bajio), obtained from the four first bordered plants in each plot in the second replication by its respective ratio to the average leaf area per plant in the first replication, as described by Francis et al. (6). The SLW was measured by taking a 1.819-cm-diameter leaf disc midway between the margin and midrib in the center of the leaf from the four uppermost leaves of the first four bordered plants. The discs were dried at 70 C for 96 hours and weighed.

Deficiency symptoms (DS), nitrogen content per unit leaf area (N-mg dm^{-2}), and potassium content per unit leaf area (K-mg dm^{-2}) were also measured shortly after anthesis. N-mg dm^{-2} was measured by micro-Kjeldahl analysis of one-half of the discs used for SLW. The K-mg dm^{-2}

was measured by determining the potassium content of the remaining one-half of the leaf discs. The leaf discs were dry-ashed and K was measured on a flamephotometer. N-mg dm⁻² and K-mg dm⁻² were measured at Manhattan only.

Plant height (PH) was the distance from the soil surface to the base of the tassel. Plant number (PN) was recorded at Tlaltizapan only, as described above. Yield per plant (YP) at Manhattan and at Tlaltizapan was measured as outlined above and expressed in grams per plant. Grain size (100-KW) was measured by weighing 100 kernels taken at random from the bulk of all kernels from all harvested ears in each plot. Kernel number (KN) was measured by dividing YP by 100-KW. Yield efficiency (YE) was measured by dividing YP by the average leaf area per plant (LA).

Correlation analyses were conducted separately to determine relationships of each of the variables with YP and YE at each location.

Experiment II

Selections were made among the 100 families in each population for specific and wide adaptation by Khan (11). For specific adaptation, the ten best families were selected from each population on the basis of YP and YE at each location. For wide adaptation, two distinct synthetics were developed from each population, one on the basis of YP and YE over all locations regardless of the coefficient of variation, and the other on the basis of the same selection criterion, but a lower coefficient of variation. The ten best families were selected in each case.

The ten families selected for each criterion were grown during October 1974 to March 1975 at Tlaltizapan. Synthetic hybrids were

developed by pollinating the plants of each of the ten families with their bulked pollen. Fifteen synthetics were produced and designated K₁, K₂, K₃, K₄, K₅, M₁, M₂, M₃, M₄, M₅, A₁, A₂, A₃, A₄, and A₅. K, M and A referred to the original populations, KDS, Mex-Mix, and Amarillo-Bajio, respectively. Subscripts 1, 2, 3, 4, and 5 referred to Manhattan specific adaptation, St. John (Kansas) specific adaptation, Tlaltizapan specific adaptation, wide adaptation without consideration of coefficient of variation and wide adaptation with consideration of lower coefficient of variation, respectively. These synthetics were evaluated at Manhattan and St. John, Kansas, and Tlaltizapan, Mexico, during summer 1975. Methods were the same as those for evaluation of the families during 1974, except that number of replications was increased from two to four at all locations and plot size was increased from two rows to four rows at the Kansas locations. Plant leaf area was measured by multiplying the leaf area factor (6) computed from leaf 8 (flag leaf = no. 1) in the first replication by the average area of leaf 8 in the other replications. Grain yield per plant (YP) was measured on all bordered plants in each plot at maturity and adjusted to 15.5% moisture percentage.

RESULTS AND DISCUSSION

Experiment I

Population means and standard deviations of variables observed in all three populations at both locations during summer 1974 are shown in Table 1. Correlation analyses of the relationships of grain yield per plant (YP) and yield efficiency (YE) with other observed characters are shown in Table 2. YP and YE were positively and highly significantly correlated in all populations at both locations. Similar correlation

Table 1. Population means and standard deviations of variables observed in 100 families in three maize populations at Manhattan, Kansas, and Tlaltizapan, Mexico, during 1974

| Data | Population | Manhattan | | Tlaltizapan | |
|---------------------------|----------------|-----------|----------|-------------|----------|
| | | mean | σ | mean | σ |
| YP (g) | P ₁ | 99.5 | 13.0 | 101.4 | 19.8 |
| | P ₂ | 95.0 | 15.8 | 161.4 | 18.1 |
| | P ₃ | 74.1 | 15.2 | 132.2 | 16.4 |
| LAI (ratio) | P ₁ | 3.4 | 0.4 | 2.8 | 0.3 |
| | P ₂ | 5.0 | 0.4 | 3.8 | 0.3 |
| | P ₃ | 4.6 | 0.5 | 3.6 | 0.4 |
| YE (g m ⁻²) | P ₁ | 164.1 | 26.7 | 193.3 | 33.3 |
| | P ₂ | 106.1 | 18.6 | 229.1 | 24.2 |
| | P ₃ | 90.4 | 22.8 | 198.2 | 27.1 |
| 100-KW (g) | P ₁ | 28.7 | 1.9 | --- | --- |
| | P ₂ | 28.0 | 2.1 | --- | --- |
| | P ₃ | 31.1 | 2.4 | --- | --- |
| KN (number) | P ₁ | 351 | 55 | --- | --- |
| | P ₂ | 342 | 55 | --- | --- |
| | P ₃ | 241 | 55 | --- | --- |
| SLW (g dm ⁻²) | P ₁ | 0.649 | 0.027 | 0.616 | 0.053 |
| | P ₂ | 0.643 | 0.028 | 0.705 | 0.048 |
| | P ₃ | 0.658 | 0.027 | 0.680 | 0.038 |
| N-mg dm ⁻² | P ₁ | 96.7 | 6.9 | --- | --- |
| | P ₂ | 97.9 | 5.9 | --- | --- |
| | P ₃ | 102.9 | 6.8 | --- | --- |
| K-mg dm ⁻² | P ₁ | 4.97 | 0.68 | --- | --- |
| | P ₂ | 5.18 | 0.85 | --- | --- |
| | P ₃ | 5.48 | 1.00 | --- | --- |
| FD (days) | P ₁ | 70 | 2 | --- | --- |
| | P ₂ | 66 | 1 | --- | --- |
| | P ₃ | 80 | 2 | --- | --- |
| PH (cm) | P ₁ | 180 | 13 | 185 | 12.7 |
| | P ₂ | 210 | 12 | 227 | 8.9 |
| | P ₃ | 234 | 15 | 246 | 8.4 |

Population P₁, P₂ and P₃ refer to KDS, Amarillo-Bajio, and Mex-Mix, respectively.

Table 2. Correlation coefficients of YP and YE with variables in 100 families in three maize populations at Manhattan, Kansas, and Tlaltizapan, Mexico, during 1974

| Data | Population | Manhattan | | Tlaltizapan | |
|-----------------------|----------------|-----------|---------|-------------|---------|
| | | YP | YE | YP | YE |
| -----r----- | | | | | |
| YP | P ₁ | 1.00** | 0.75** | 1.00** | 0.78** |
| | P ₂ | 1.00** | 0.86** | 1.00** | 0.51** |
| | P ₃ | 1.00** | 0.90** | 1.00** | 0.65** |
| LAI | P ₁ | 0.11 | -0.56** | 0.50** | -0.09 |
| | P ₂ | 0.22* | -0.27** | 0.29** | -0.48** |
| | P ₃ | -0.25* | -0.62** | 0.33** | -0.49** |
| 100-KW | P ₁ | -0.05 | 0.01 | -- | -- |
| | P ₂ | 0.26** | 0.23** | -- | -- |
| | P ₃ | -0.12 | -0.09 | -- | -- |
| KN | P ₁ | 0.90** | 0.66** | -- | -- |
| | P ₂ | 0.86** | 0.76** | -- | -- |
| | P ₃ | 0.93** | 0.83** | -- | -- |
| SLW | P ₁ | 0.01 | 0.00 | 0.22* | 0.14 |
| | P ₂ | 0.16 | 0.19 | 0.15 | 0.07 |
| | P ₃ | 0.10 | 0.19 | 0.12 | 0.15 |
| N-mg dm ⁻² | P ₁ | -0.02 | 0.01 | -- | -- |
| | P ₂ | 0.21* | 0.12 | -- | -- |
| | P ₃ | -0.04 | -0.02 | -- | -- |
| K-mg dm ⁻² | P ₁ | -0.03 | -0.01 | -- | -- |
| | P ₂ | -0.08 | -0.13 | -- | -- |
| | P ₃ | 0.07 | 0.04 | -- | -- |
| FD | P ₁ | -0.20* | -0.24* | -- | -- |
| | P ₂ | -0.20* | -0.29** | -- | -- |
| | P ₃ | -0.38** | -0.49** | -- | -- |
| PH | P ₁ | 0.07 | -0.11 | 0.67** | 0.36** |
| | P ₂ | -0.01 | -0.07 | 0.03 | -0.07 |
| | P ₃ | -0.30** | -0.30** | 0.25* | -0.01 |

Population P₁, P₂, and P₃ refer to KDS, Amarillo-Bajio and Mex-Mix, respectively.

* r significant at 0.05 probability level.

** r significant at 0.01 probability level.

coefficients have been reported by Buren et al. (3).

100-KW varied independently of YP and YE in KDS and Mex-Mix, but was associated with YE ($r = 0.23^*$) and YP ($r = 0.26^{**}$) in Amarillo-Bajio. KN, on the other hand, was closely associated with YP and also was highly associated with YE in all three populations. Tanaka and Yamaguchi (17) reported positive correlations between KN and YP, but no associations between kernel size (100-KW) and YP. Yamaguchi (21) observed positive associations of both KN and 1000-KW with YP, but the magnitude of the correlation coefficient was much lower between 1000-KW and YP than between KN and YP. He also observed that 1000-KW affected grain yield in some varieties (20). It is apparent that grain yield in maize is highly determined by kernel number. However, depending on genetic make up of the varieties, kernel size may also contribute considerably to grain yield.

The relationship between LAI and YP was positive in all three populations ($r = 0.50^{**}$ in KDS, 0.29^{**} in Amarillo-Bajio, and 0.33^{**} in Mex-Mix) at Tlaltizapan. At Manhattan, correlation coefficients were positive in Amarillo-Bajio ($r = 0.22^*$), and in KDS ($r = 0.11$), and negative in Mex-Mix ($r = -0.25^*$). A positive association between grain yield and leaf area index was reported by Yamaguchi (21). It suggests that the families were tested at suboptimal LAI. Consequently, those families that had larger LAI intercepted more radiation and produced higher grain yields. The non-association in KDS and the negative association in Mex-Mix may indicate the families developed a LAI within the range of the optimum and above the optimum, respectively (5). However, since Mex-Mix showed an extreme photoperiod sensitivity at Manhattan - it

grew taller, developed thicker stem and larger number of leaves, flowered later, and had more senesced leaves slightly after anthesis than the other populations -, the negative association between LAI and YP is likely incidental. This is strongly supported by the positive correlation between LAI and 50% silking date ($r = 0.44^{**}$) and the higher magnitude of the negative correlation between 50% silking date and YP in this population at Manhattan.

Negative and highly significant associations occurred between LAI and YE in all populations and locations except in KDS at Tlaltizapan. The insignificant relationship between LAI and YE in KDS at Tlaltizapan was likely caused by the soil nutrient imbalance that limited LAI, PH, YP, and YE. Correlation coefficients between DS and each of these variables were, respectively, -0.37^{**} , -0.68^{**} , -0.64^{**} , and -0.48^{**} .

Negative relationships between LAI and YE have been reported in density trials by Tanaka and Yamaguchi (17). Since grain yield is determined by both 100-KW and KN, negative correlations between LAI and either 100-KW or KN or both might be expected (17). Variation in LAI in the present study was caused by genetic differences among families, not by environmental differences among planting densities, and significant correlations were not observed except in Mex-Mix ($r_{LAI/KN} = -0.22^{*}$). This lone negative correlation was probably caused by the negative correlation between LAI and YP in this population.

Higher yielding families possessed either of two traits measured in these studies. They developed larger LAI and intercepted more solar radiation or produced larger grain weight per unit leaf area. Families in the former group are likely to be less density responsive. Their

already larger LAI would rapidly reach the optimum with increasing density. This probably explains why contemporary maize cultivars, mainly selected on the basis of YP, thus, larger LAI, give limited responses to increased density (1, 17, 19). Yield-efficient families, on the other hand, would likely be density responsive. Their lower LAI at standard plant densities is likely preventing them from reaching higher grain yield levels. They appear to require higher plant densities than usual for maximum grain yield (3, 17, 21).

Plant traits that cause high YE were not elucidated clearly. Leaf thickness (SLW) was not associated with either YP or YE in any population. SLW, however, appeared to influence 100-KW ($r = 0.20^*$, 0.21^* , and 0.12 in Amarillo-Bajio, Mex-Mix, and KDS, respectively) more than KN ($r = 0.05$, 0.02 , and 0.03 in KDS, Amarillo-Bajio and Mex-Mix, respectively).

Nitrogen content per unit leaf area (N-mg dm^{-2}) and potassium content per unit leaf area (K-mg dm^{-2}) were not significantly related to YP and YE in the three populations except in Amarillo-Bajio. A significant correlation was observed between N-mg dm^{-2} and YP in this population.

The effects of nutrients status on leaf photosynthesis of maize plant have been discussed by Moss and Doyle (13). Also, SLW has been reported to be associated with photosynthesis per unit leaf area in other species (2, 10, 14). In this study, it was associated with N-mg dm^{-2} ($r = 0.44^{**}$, 0.43^{**} , and 0.39^{**} in KDS, Amarillo-Bajio and Mex-Mix, respectively) in all three populations at Manhattan. The lack of consistent relationships of SLW, N-mg dm^{-2} and K-mg dm^{-2} with YP and YE probably indicates that leaf photosynthetic rate was not the factor

limiting grain yields. There is, however, some indications that leaf thickness (SLW) may contribute to 100-KW which, together with KN, determines grain yield. However, the populations in which the relationship was observed, Amarillo-Bajio and Mex-Mix, were recently introduced and may have lacked adaptation. Investigations with adapted populations are needed to determine the contribution of SLW to grain yield in maize.

Negative relationships, significant to highly significant, were observed between 50% silking date (FD) and YP and YE in all three populations at Manhattan. Late flowering families encountered more unfavorable conditions or had a briefer period of grain filling. The yield component that was most affected by late flowering was KN ($r_{FD/KN} = -0.20^*$ in KDS, -0.19 in Amarillo-Bajio, and -0.32^{**} in Mex-Mix, respectively).

Plant height (PH) at Manhattan varied independently with YP and YE in KDS and Amarillo-Bajio. It was negatively and highly significantly associated with YP and YE in Mex-Mix. At Tlaltizapan it was positively associated with YP in KDS and Mex-Mix ($r = 0.67^{**}$ and 0.25^* , respectively), but varied independently of YP in Amarillo-Bajio. It varied independently of YE in all three populations except in KDS, where a correlation coefficient, $r = 0.36^{**}$, was observed. The positive association between PH and YE in KDS at Tlaltizapan was likely incidental for the reasons given above. The lack of consistency in the relationships of PH and YP and YE in all three populations at all locations indicates that the effect of PH on YP and YE is dependent on genotype and environment and cannot be generalized.

Experiment II

This experiment evaluated interrelationships of selection criteria of YP, YE, and associated factors in the families on performance of the

derived synthetics at Manhattan and St. John, Kansas. Plants at Tlaltizapan, Mexico, were infected with severe maize stunt virus and were not harvested for yield.

Yield per plant (YP), yield efficiency (YE), kernel size (100-KW), and kernel number (KN) of the synthetics and original populations (referred to by the subscript 0) observed at Manhattan and St. John are shown in Table 3.

Yield components did not differ significantly among the entries in each population at both locations except for 100-KW in Amarillo-Bajio and KN in Mex-Mix. The 100-KW was significantly greater in A_2 than A_1 and A_0 . In Mex-Mix, significant differences in KN occurred between M_1 , M_4 , and M_5 and M_0 , M_2 , and M_3 at Manhattan, and between M_1 and M_4 , M_0 and M_2 , and M_5 and M_0 at St. John.

Kernel size (100-KW) had little effect on YP and YE. Its significant differences in Amarillo-Bajio did not concur with increased YP and/or YE. Kernel number, on the other hand, was positively associated with YP and YE. These results agreed with those in Experiment I and those of Tanaka and Yamaguchi (17). They, however, deviated from those reported by Yamaguchi (20, 21) as the kernel size did not affect YP and YE.

Leaf area index (LAI), specific leaf weight (SLW), nitrogen content per unit leaf area ($N\text{-mg dm}^{-2}$), and potassium content per unit leaf area ($K\text{-mg dm}^{-2}$) at both locations are shown in Table 4. Differences in SLW, $N\text{-mg dm}^{-2}$, and $K\text{-mg dm}^{-2}$ among the synthetics were insignificant in all three populations at any of the locations. Similarly, differences in LAI among synthetics and between individual synthetics and K_0 in KDS at St. John were insignificant. At Manhattan, however, the synthetics

Table 3. Yield per plant (YP), yield efficiency (YE), kernel size (100-KW), and kernel number (KN) of original populations and their derived synthetics at Manhattan and St. John, Kansas, during 1975

| Population | Synthetics | Manhattan | | | St. John | | |
|--------------------|----------------|-----------|----------------------|--------|----------|----------------------|--------|
| | | YP | YE | 100-KW | YP | YE | 100-KW |
| | | (g) | (g m ⁻²) | (g) | (g) | (g m ⁻²) | (g) |
| KDS | K ₀ | 119.0 | 202.8 | 29.4 | 116.3 | 190.1 | 27.5 |
| | K ₁ | 134.5 | 179.7 | 30.1 | 113.9 | 173.0 | 28.2 |
| | K ₂ | 113.0 | 150.6 | 31.2 | 96.7 | 143.2 | 27.9 |
| | K ₃ | 132.0 | 166.2 | 30.5 | 118.8 | 178.5 | 27.6 |
| | K ₄ | 117.5 | 158.7 | 31.7 | 123.0 | 180.5 | 29.3 |
| | K ₅ | 118.0 | 167.7 | 29.3 | 103.5 | 138.1 | 29.0 |
| | LSD .05 | ns | ns | ns | ns | ns | ns |
| Amarillo- Bajio | A ₀ | 114.3 | 145.5 | 29.6 | 113.3 | 133.0 | 30.0 |
| | A ₁ | 108.4 | 110.7 | 29.2 | 95.9 | 119.3 | 29.6 |
| | A ₂ | 111.8 | 106.1 | 32.7 | 112.3 | 135.8 | 31.2 |
| | A ₃ | 108.7 | 128.4 | 30.9 | 99.4 | 118.8 | 28.6 |
| | A ₄ | 119.9 | 148.6 | 30.8 | 102.2 | 131.4 | 29.0 |
| | A ₅ | 114.5 | 131.5 | 31.2 | 127.1 | 139.3 | 32.0 |
| | LSD .05 | ns | ns | 1.8 | ns | ns | ns |
| Mex-Mix | M ₀ | 84.4 | 89.6 | 30.9 | 50.7 | 76.3 | 29.0 |
| | M ₁ | 103.1 | 110.9 | 31.2 | 77.7 | 115.6 | 28.7 |
| | M ₂ | 75.5 | 74.2 | 30.7 | 55.0 | 73.1 | 27.7 |
| | M ₃ | 77.2 | 76.8 | 32.6 | 67.7 | 85.8 | 29.5 |
| | M ₄ | 109.5 | 122.5 | 32.0 | 79.4 | 97.8 | 29.0 |
| | M ₅ | 101.7 | 110.0 | 31.2 | 72.8 | 101.2 | 30.6 |
| | LSD .05 | 13.9 | 18.6 | ns | 18.8 | 21.6 | ns |
| | | | | | | | 55 |

Table 4. Leaf area index (LAI), specific leaf weight (SLW), and nitrogen content per unit leaf area (N-mg dm⁻²) of original populations and their derived synthetics at Manhattan and St. John, Kansas, during 1975

| Population | Synthetic | Manhattan | | | St. John | | |
|----------------|-----------|-----------|------------------------|------------------------|------------------------|------------------------|------------------------|
| | | LAI | SLW | N | LAI | SLW | N |
| | | | (mg dm ⁻²) | (mg dm ⁻²) | (mg dm ⁻²) | (mg dm ⁻²) | (mg dm ⁻²) |
| KDS | K0 | 3.25 | 0.618 | 104.4 | -- | 3.48 | 89.8 |
| | K1 | 4.18 | 0.623 | 111.5 | -- | 3.68 | 93.6 |
| | K2 | 4.22 | 0.633 | 109.8 | -- | 3.77 | 88.4 |
| | K3 | 4.16 | 0.621 | 118.6 | -- | 3.70 | 72.3 |
| | K4 | 4.15 | 0.628 | 114.6 | -- | 3.81 | 76.7 |
| | K5 | 3.93 | 0.598 | 113.6 | -- | 4.19 | 77.9 |
| | LSD .05 | 0.31 | ns | ns | -- | ns | ns |
| Amarillo-Bajio | A0 | 4.38 | 0.679 | 101.2 | 2.76 | 4.74 | 102.5 |
| | A1 | 5.54 | 0.645 | 100.1 | 2.17 | 4.46 | 90.1 |
| | A2 | 5.89 | 0.647 | 104.6 | 2.09 | 4.61 | 100.2 |
| | A3 | 4.70 | 0.652 | 98.5 | 2.30 | 4.65 | 89.8 |
| | A4 | 4.55 | 0.681 | 107.7 | 2.21 | 4.34 | 85.4 |
| | A5 | 4.86 | 0.698 | 112.1 | 2.15 | 5.08 | 89.2 |
| | LSD .05 | 0.56 | ns | ns | ns | 0.44 | ns |
| Mex-Mix | M0 | 5.25 | 0.628 | 132.9 | -- | 3.67 | 80.0 |
| | M1 | 5.20 | 0.654 | 136.6 | -- | 3.68 | 81.4 |
| | M2 | 5.71 | 0.658 | 159.1 | -- | 4.18 | 98.8 |
| | M3 | 5.63 | 0.645 | 150.4 | -- | 4.39 | 82.8 |
| | M4 | 4.99 | 0.628 | 127.9 | -- | 4.53 | 94.1 |
| | M5 | 5.15 | 0.670 | 144.1 | -- | 4.00 | 87.8 |
| | LSD .05 | ns | ns | ns | -- | 0.49 | ns |

individually developed a LAI larger than that of K_0 , but did not differ significantly from each other. In Amarillo-Bajio, LAI differed significantly among synthetics as well as between some individual synthetics and A_0 at Manhattan. The LAI's of A_1 and A_2 were similar but significantly greater than that of any other synthetic and A_0 . At St. John, a significant difference in LAI was observed only between A_5 and each of the following synthetics: A_1 , A_2 and A_4 . All the synthetics displayed a LAI that was similar to that of A_0 . Mex-Mix synthetics and M_0 developed a similar LAI at Manhattan. However, significant differences occurred at St. John among synthetics and between some individual synthetics and M_0 . The LAI's of M_2 , M_3 , and M_4 were greater than those of M_0 and M_1 , but similar to that of M_5 except for M_4 .

SLW, N-mg dm⁻², and K-mg dm⁻² did not affect YP and YE. Significant differences in YP and YE in Mex-Mix at St. John did not concur with significant differences in those variables. This was illustrated in Experiment 1 by lack of correlation between these variables and YP and YE in Mex-Mix.

Larger LAI did not always correspond with higher YP. Significant differences in KDS at Manhattan and in Amarillo-Bajio at both locations did not coincide with significant differences in YP. Significant differences in YP in Mex-Mix at Manhattan also did not coincide with differences in LAI. This was also true even in Mex-Mix at St. John where both LAI and YP differed significantly, but the higher yielding synthetics did not always display a larger LAI. YE seemed to contribute negatively to the effect of LAI. Larger LAI and corresponding smaller YE accounted for lack of significant differences in YP in KDS at Manhattan and in Amarillo-Bajio at both locations. In Mex-Mix, small variations in LAI among all

entries at Manhattan and between M_0 and M_1 and among M_2 , M_3 , and M_5 at St. John without corresponding variations in YE and differences in LAI between M_0 and M_4 at St. John accounted for significant differences in YP.

As in Experiment I, high yielding ability appeared related to two mechanisms: large LAI for increased light interception efficiency, and high yield efficiency for increased light utilization for grain production.

The effect of the combined selection criteria for YP and YE appeared to depend on populations. LAI was increased but YP and YE were unaffected in KDS and Amarillo-Bajio, particularly at Manhattan. YP and YE were increased but LAI was affected only slightly in Mex-Mix at both locations.

Non-response to selection for YP in KDS and Amarillo-Bajio may be attributed to insufficient selection pressure and insufficient selection cycles. Lack of improvement in YE can be attributed to insufficient selection pressure or operation of YP and YE against YE. The last mechanism is the most likely, since LAI increased significantly due to selection in these two populations. Positive associations between YP and LAI and negative associations between YE and LAI in Experiment I would lead to unchanged, increased, or decreased LAI if the weight of YP was equal to, greater than, or smaller than that of YE in the selection criterion.

Positive responses to selection for both YP and YE in Mex-Mix appeared to be attributable to large genetic variability. Thus, applied selection pressure increased YP and YE in a single selection cycle in

some synthetics. Equal weight of YP and YE in the selection criterion was also important. This was illustrated in Experiment I by negative associations between LAI and both YP and YE and by a closer positive correlation coefficient between YP and YE at Manhattan.

The combined selection criterion for YP and YE was likely detrimental to YE. Its positive response for both characters seemed to require a relationship of LAI and both YP and YE to be of the same sign. This was unlikely to occur with well adapted populations as shown in Experiment I. The case observed in Mex-Mix in the temperate environment might be incidental, caused by photoperiod sensitivity and the presence of tropical genes in this population. If the goal is to maximize grain yield at the selection density, YP alone is likely the most suitable selection criterion. If, on the other hand, the goal is to maximize utilization of solar radiation for grain production by thicker planting densities, YE is likely the most suitable selection criterion.

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RELATIONSHIP AMONG VEGETATIVE CHARACTERISTICS, TRANSLOCATION, AND YIELD EFFICIENCY IN THREE MAIZE POPULATIONS

Yield efficiency of maize has been reported to be associated with density tolerance (2, 10). Since it is a ratio of grain yield to leaf area per plant, it may also be a criterion for increasing the limiting grain sink capacity in maize (4, 5, 10, 11).

Physiological traits affecting yield efficiency were not clearly elucidated in our previous studies (8). We, therefore, compared dry matter production and partitioning among the populations used and between the original populations and their derivative synthetics (8). Plant vegetative characteristics, translocation efficiency, and yield efficiency--relationships important in predicting the behavior of maize at different planting densities--were investigated.

MATERIALS AND METHODS

The original populations and synthetics used have been described (8). Only the Manhattan specific adaptation synthetics, K_1 , A_1 , and M_1 , were compared with their respective original population, K_0 , A_0 , and M_0 , for dry matter production and partitioning throughout the growing season. They were grown at Manhattan, Kansas, during 1975. The field design was a split-plot, with populations the main plots and synthetics and original populations the sub-plots. Cultural methods were the same as for the previous experiment (8) at Manhattan and St. John, Kansas, in 1975 except that replications were decreased from four to three and plot size was increased from four rows to eight rows. The six bordered rows were sampled.

Six harvests were taken at approximately 3-week intervals. At each harvest, five plants bordered by other plants in each plot were cut at ground level. Plant leaf area (L) was measured with a LI-3000 Lambda Instrument Co. meter. Shoots were dried at 70C to constant weight and weighed (TDW = total plant dry weight). After anthesis, plants were separated into plant vegetative parts (VDW = leaf, leaf sheath, stalk, and tassel) and ear parts (EW = husks, cob, shank, and grain). Their dry weight and the tassel dry weight (TW) were measured separately.

The following variables were computed: total plant dry weight at silking (DWS), plant dry weight produced after silking (DAS = TDW at harvest - DWS), dry weight production efficiency after silking (DWE = DAS/leaf area duration after silking), translocation efficiency (TE = ear dry weight at maturity x 100/DAS), yield efficiency on the basis of leaf area per plant at silking (YE_L = grain yield at harvest/leaf area at silking), yield efficiency on the basis of leaf area duration after silking (YE_D = grain yield at harvest/leaf area duration after silking), and harvest index (HI = grain yield at harvest/total plant dry weight at harvest).

Leaf area duration after silking (D), mean growth rate (\bar{G}), and net assimilation rate (E) from 52 to 110 days after sowing were measured according to Radford (9); the following formulae were used (t is days after sowing): $D = \int_{t_1}^{t_2} L dt$; $\bar{G} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{dTDW}{dt}$; and $E = \frac{b+2 ct}{a'+b'+c't^2}$. For computing E, relationships between TDW and t and between L and t were first studied. They fitted curves of the form $TDW = a + bt + ct^2$ and $L = a' + b't + c't^2$. The coefficients, a, b, c, a', b', and c', were determined for each population.

Correlation studies were conducted with the data from the six entries used in this experiment to simulate heterogenous population as used by breeders in beginning selection programs. Relationships studied were DWS, DAS, DWE, TE and D with TW and EW and YE_L , HI, and D with TE and YE_D .

RESULTS AND DISCUSSION

Developmental patterns of all six entries are shown in Table 1. The three populations differed in their 50% silking days after sowing. The KDS population flowered earlier, Mex-Mix flowered later, and Amarillo-Bajio was intermediate. The original population (syn-0) and synthetic (syn-1) flowered nearly simultaneously in each population.

The populations differed in growth duration. KDS matured earliest; Mex-Mix and Amarillo-Bajio were later, but did not differ from each other. The syn-1's matured concurrently with the syn-0's within populations except in KDS. Growth duration was delayed about one week longer for K_1 than for K_0 .

Grain yield per plant (YP), yield efficiency on the basis of leaf area at silking (YE_L), and harvest index (HI) of the entries are shown in Table 2.

The YP of the three populations was similar. The syn-1's yielded 27% more than the syn-0's across all populations. Individual syn-1's did not differ statistically from their respective syn-0's within individual populations, but YP was greater for the former than for the latter.

The KDS population was most yield efficient. Its YE_L was larger than that of the two other populations. Amarillo-Bajio and

Table 1. 50% silking days after sowing and growth duration of synthetic hybrids and original populations at Manhattan, Kansas, during 1975

| Entry | 50% silking | growth duration |
|----------------|-----------------------------|-----------------|
| | -----days after sowing----- | |
| K ₀ | 74 | 118 |
| K ₁ | 73 | 125 |
| A ₀ | 78 | 132 |
| A ₁ | 78 | 132 |
| M ₀ | 81 | 132 |
| M ₁ | 80 | 132 |

Table 2. Grain yield per plant (YP), grain yield per unit leaf area at silking (YE_L), and harvest index of synthetic hybrids and original populations at Manhattan, Kansas, during 1975

| Entry | YP | YE_L | HI |
|-------|-------|-------------|------|
| | g | $g\ m^{-2}$ | -- |
| K_0 | 129.6 | 195.8 | 0.41 |
| K_1 | 155.9 | 210.1 | 0.37 |
| A_0 | 138.3 | 144.3 | 0.31 |
| A_1 | 154.8 | 151.4 | 0.33 |
| M_0 | 94.0 | 116.6 | 0.25 |
| M_1 | 148.9 | 160.4 | 0.36 |

Mex-Mix had similar YE_L . The YE_L did not differ between the syn-0's and syn-1's across all populations or within individual populations.

Harvest index (HI) was similar for KDS and Amarillo-Bajio and for Mex-Mix and Amarillo-Bajio, but was lower for Mex-Mix than for KDS. Mean HI of all populations did not differ between the syn-0's and syn-1's, but within individual populations HI was larger in M_1 than in M_0 .

Changes in plant dry matter from 31 days after planting to maturity are shown in Figure 1. The six entries had similar dry matter accumulation patterns until 94 days after planting, but differed from then to maturity. The KDS population accumulated less dry matter than the other populations; it also matured earliest. Amarillo-Bajio and Mex-Mix were similar in growth duration and in dry matter accumulation. Differences in dry matter accumulation between the original populations and synthetics varied with the populations. Dry matter accumulation was significantly greater in the synthetic than in the original population only in KDS. Dry matter accumulation was higher in the Amarillo-Bajio synthetic and lower in the Mex-Mix synthetic as compared with the original populations, but differences were not significant at 5% level. Maximum dry weight was reached 94 to 110 days after planting K_0 , K_1 , and M_1 and at maturity for the other three entries.

The average growth rate (\bar{G}) and the corresponding average grain growth rate are shown in Figures 2 and 3, respectively. In all entries, \bar{G} increased from emergence to a maximum at flowering and then declined. It remained positive to maturity in A_0 , A_1 , and M_0 . But, \bar{G} became negative during maturation of K_0 , K_1 , and M_1 . \bar{G} differed among entries only during the period of 110 days after sowing to maturity. The lowest \bar{G} , -8.3 g/plant/day, was observed in K_0 .

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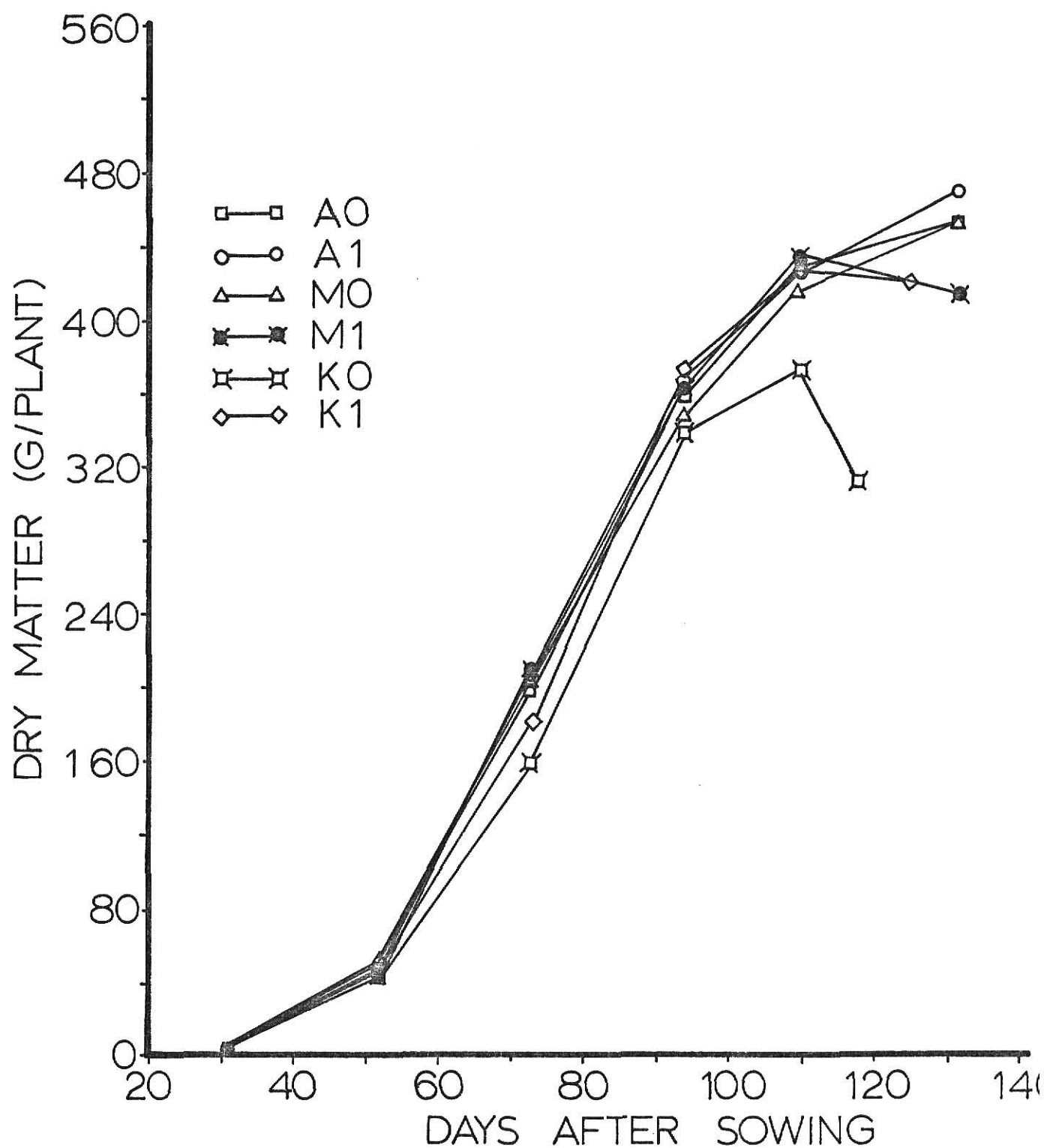


Figure 1. Total plant dry weight 31 days after sowing to maturity of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

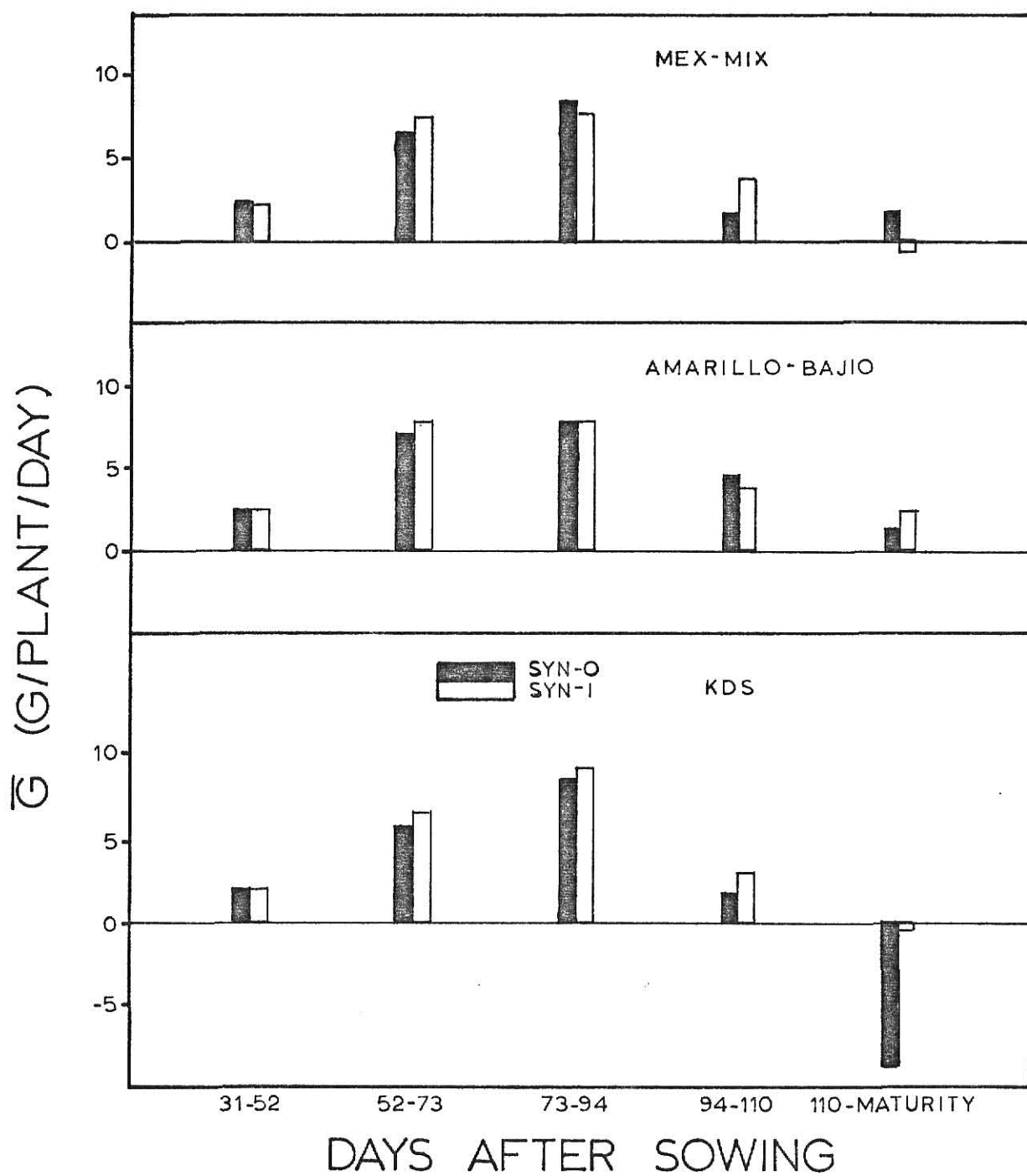


Figure 2. Average growth rate 31 days after sowing to maturity of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

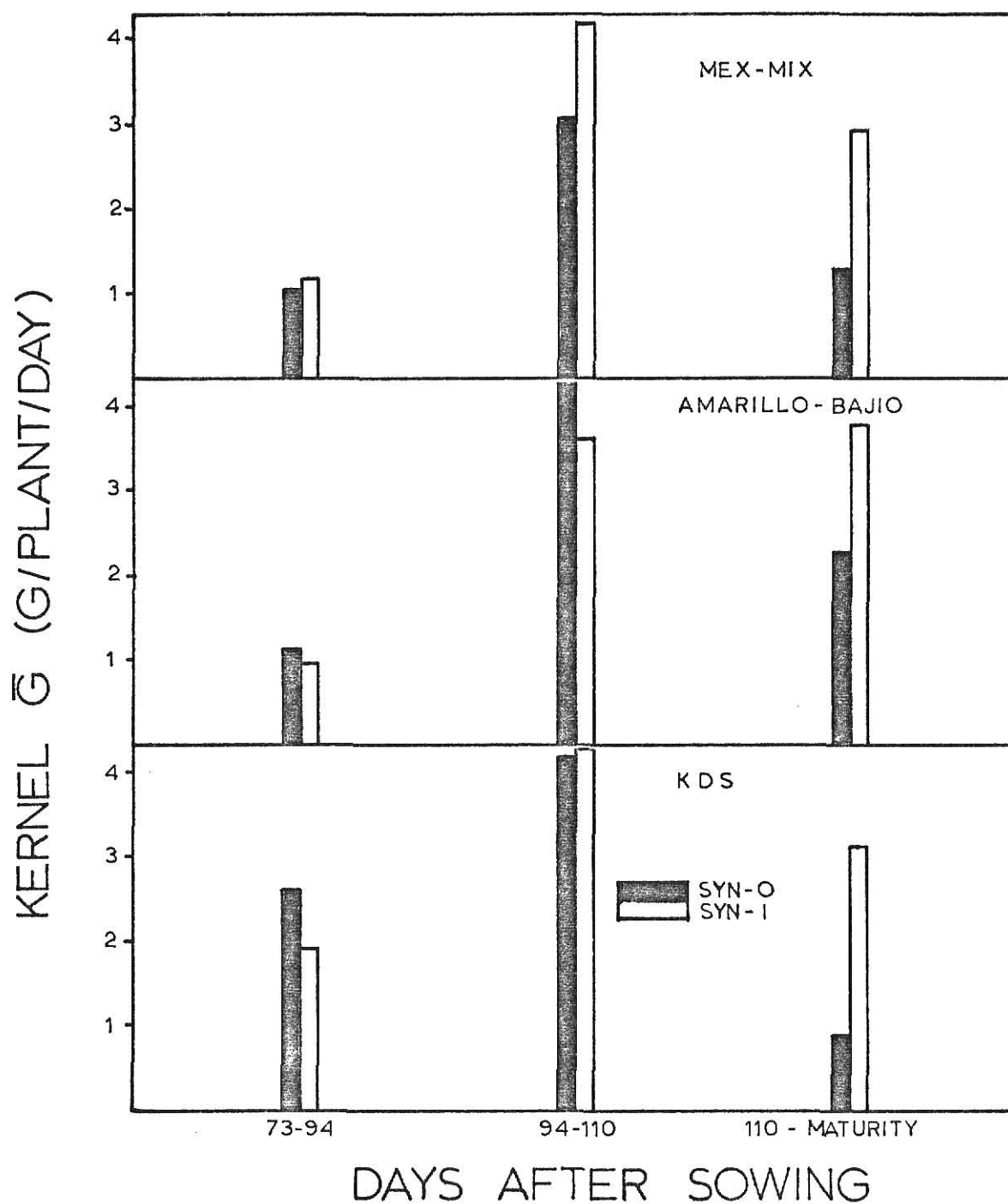


Figure 3. Average kernel growth rate 73 days after sowing to maturity of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

The grain growth rate increased after silking, 73 to 94 days after sowing, to a maximum 94 to 110 days after sowing and then declined. It remained positive up to maturity in all entries. The grain growth rate did not differ consistently between the syn-0's and syn-1's within individual populations during early grain development, but was higher in the syn-1's during late grain development.

Total plant dry weight was partitioned into plant vegetative parts (stalk, leaf sheaths, leaves, and tassel), ear vegetative parts (husks, cobs, and shanks), and grain as shown in Figure 4. Plant vegetative dry matter increased between 73 and 94 days after sowing, during which anthesis and beginning of grain filling occurred in all entries. It progressively decreased up to maturity. The decrease was most marked in K_0 and M_1 and least marked in M_0 . Less dry matter accumulated in vegetative parts of KDS than the two other populations during the two last periods of growth. Vegetative growth rate averaged over all populations did not differ between syn-1's and syn-0's at each harvest. However, at maturity, vegetative growth rates differed significantly between syn-0's and syn-1's in KDS and Mex-Mix. More dry matter was accumulated in plant vegetative parts by K_1 than by K_0 . In Mex-Mix, however, more vegetative dry matter was accumulated by the original population than by the synthetic.

Ear vegetative dry weight increased from 52 to 73 and 73 to 94 days after sowing. Anthesis and beginning of grain filling occurred in all entries during that time. It remained almost constant thereafter except in K_0 and M_0 . Ear vegetative parts decreased in weight between 110 and 118 days after sowing in K_0 ; whereas, in M_0 , weight of ear

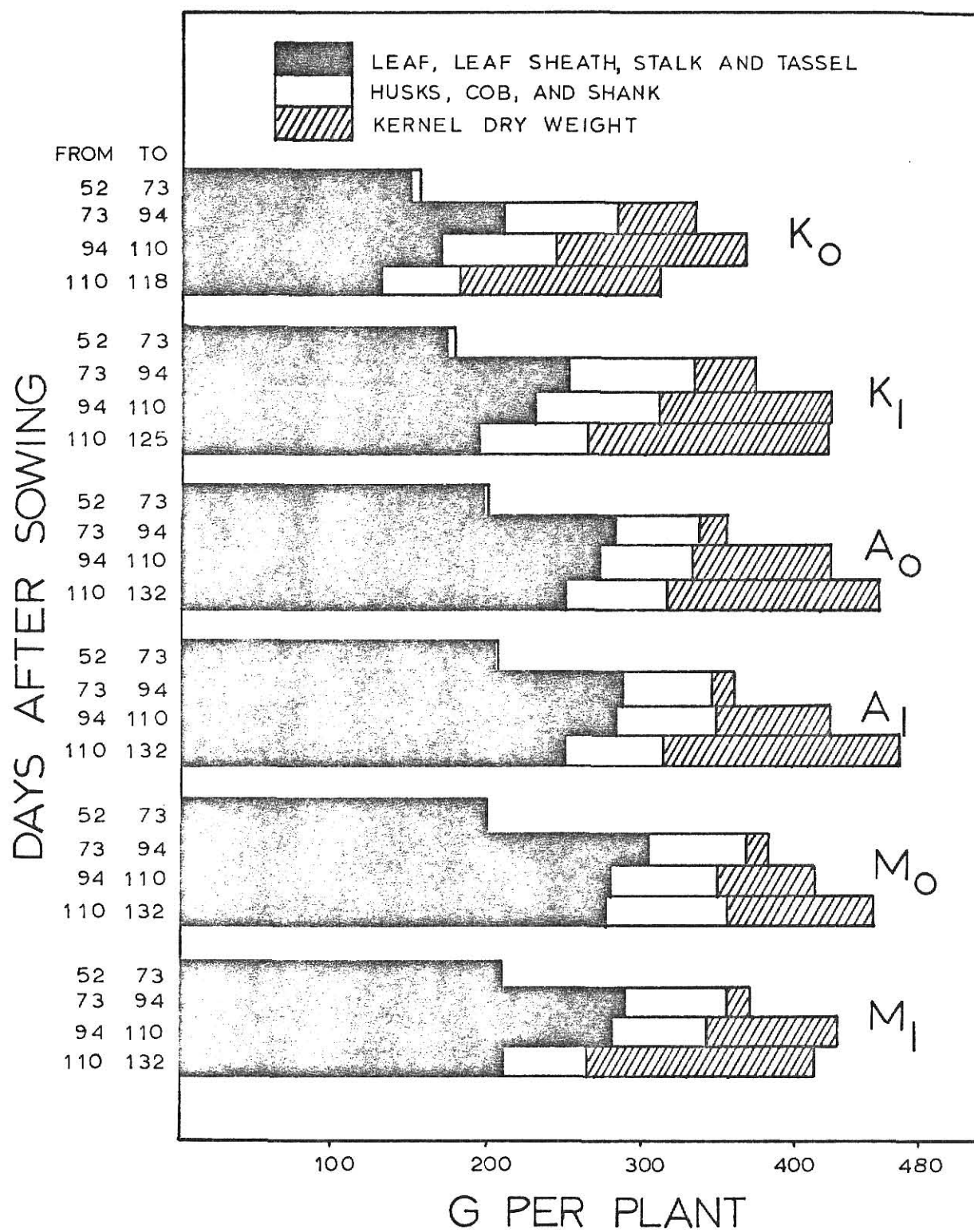


Figure 4. Dry matter partitioning 52 days after sowing to maturity of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

vegetative parts increased to maturity. Grain dry weight, on the other hand, increased from the beginning of grain filling to maturity.

Decreased plant vegetative dry weight while grain dry weight increased suggested retranslocation of assimilates from plant vegetative parts to the filling kernels. This was strongly supported by the negative \bar{G} during maturation of some entries. The contribution of the stalk to the developing kernels has been reported by Daynard et al. (3) and Hume et al. (7). Ear dry matter was a product of only a fraction of photosynthesis after silking in A_0 , A_1 , and M_0 , total photosynthesis after silking in K_1 and M_1 , and photosynthesis prior and after silking in K_0 .

The grain sink appeared smaller than the source in A_0 , A_1 , and M_0 ; hence, a portion of assimilates produced after silking was stored in vegetative parts at maturity. Sink and source were equal in K_1 and M_1 and most of the assimilates produced after silking were used for ear and grain growth. The sink was probably larger than the source in K_0 so that assimilates stored in vegetative parts prior to silking were additionally retranslocated to the ear to sustain ear and kernel growth. Smaller grain sink than source capacity has been reported by Daynard et al. (3) and Goldsworthy et al. (4, 5). Hanway (6) and Allisson and Watson (1), however, did not observe accumulation of large amounts of dry matter produced after silking in vegetative parts. Maize varieties in their studies probably had similar source and sink capacities.

Leaf area (L) of all entries reached a maximum 73 to 94 days after sowing as shown in Figure 5. This period coincided with anthesis and beginning of grain filling. The maximum L combined with a large E

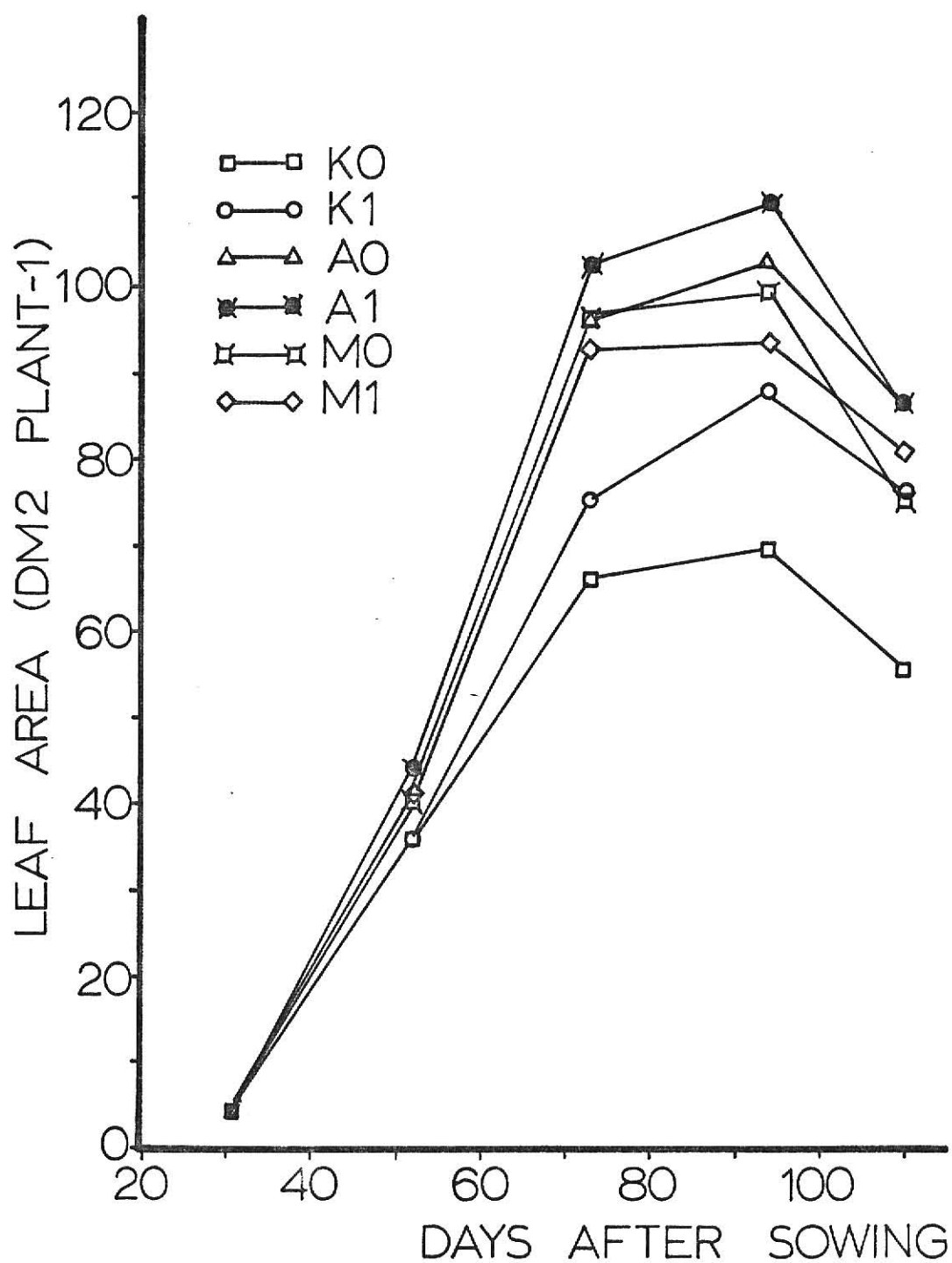


Figure 5. Leaf area per plant 31 to 110 days after sowing of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

(net assimilation rate) accounted for the maximum growth rate observed during this period ($G = L \times E$) (9).

The L was smaller for the KDS population than for the two other populations during the three last harvests shown in Figure 5. Amarillo-Bajio maintained a larger L than Mex-Mix only at 94 days after sowing. The average L across all populations was significantly larger for syn-1's than for syn-0's 94 and 110 days after sowing. Within individual populations, L was significantly larger for syn-1's as compared to syn-0's only in KDS 94 days after sowing.

Insignificant differences in dry matter accumulation and significant differences in L among entries from 73 to 110 days after sowing suggested E differed among entries as shown in Figure 6. Populations A_0 and K_0 had the highest E , M_0 and A_1 had the lowest E and K_1 and M_1 had an intermediate E .

Net assimilation rate (E) decreased in most entries 52 to 110 days after sowing, but increased in K_0 and A_0 94 and 110 days after sowing. This period corresponded with rapid grain filling. Increased E concurred with declining L but without a corresponding decline in total dry matter accumulation. A greater demand for assimilates by the rapidly growing kernels probably increased the net photosynthetic rate in the remaining L . This seems to be supported by reports from Tanaka and Yamaguchi (10) and Allisson and Watson (1), who observed an increased E when a portion of L was mechanically removed and the kernel sink was kept intact.

Table 3 shows the mean leaf area duration (D), total plant dry weight at silking (DWS), total dry weight produced after silking (DAS), dry weight production efficiency (DWE), tassel dry weight (TW), ear dry

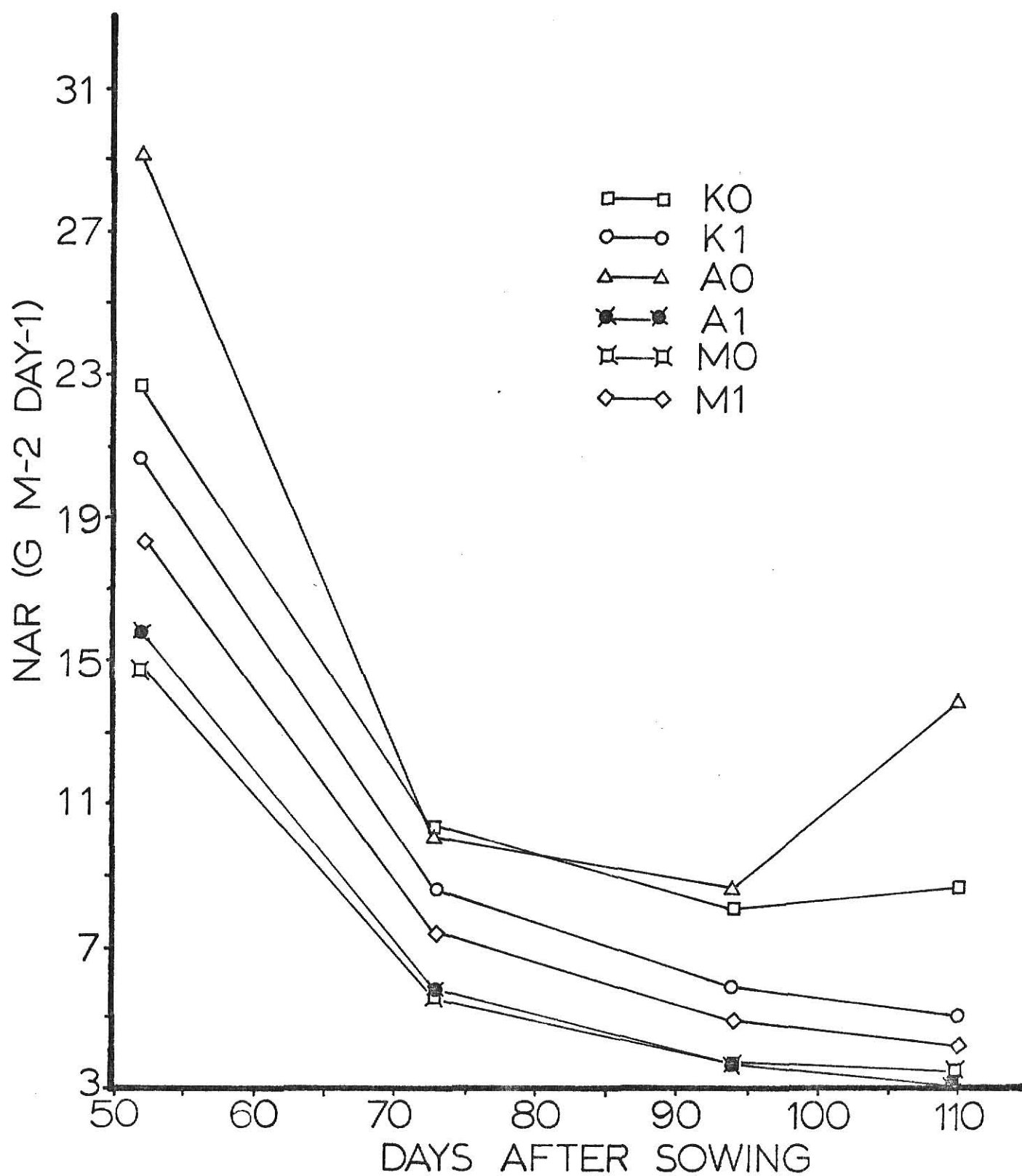


Figure 6. Net assimilation rate 52 to 110 days after sowing of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

Table 3. Leaf area duration (D), total dry weight at silking (DWS), total dry weight production after silking (DAS), dry weight production efficiency after silking (DWE), tassel dry weight (TW), ear dry weight (EW), translocation efficiency (TE), and grain yield per unit leaf area duration (YE_D) of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

| Entries | D | DWS | DAS | DWE | TW | EW | TE | YE_D |
|---------|-------|-------|-------|-----------|------|-------|-------|-----------|
| | m^2 | g | g | gm^{-2} | g | g | % | gm^{-2} |
| K_0 | 3.15 | 158.1 | 155.2 | 49.3 | 7.8 | 182.1 | 117.3 | 41.1 |
| K_1 | 4.03 | 181.6 | 238.4 | 59.2 | 10.2 | 224.4 | 94.1 | 38.7 |
| A_0 | 4.74 | 201.4 | 252.6 | 53.3 | 11.2 | 202.8 | 80.3 | 29.2 |
| A_1 | 4.94 | 206.5 | 263.6 | 53.4 | 12.8 | 220.0 | 83.5 | 31.3 |
| M_0 | 4.45 | 199.1 | 254.0 | 57.0 | 11.1 | 173.9 | 68.5 | 21.2 |
| M_1 | 4.42 | 211.1 | 203.0 | 45.9 | 11.4 | 202.9 | 100.0 | 33.7 |

weight (EW), translocation efficiency (TE), and grain yield per unit of leaf area duration (YE_D). Relationships of DWS, DAS, DWE, TE, and D with TW and EW are shown in Table 4. DWS, DAS, and D were each positively and closely correlated with TW. The correlation coefficients were highly significant except for DAS, which was significant. Insignificant positive correlation coefficients were observed between DWE and both EW and TW and a negative insignificant correlation coefficient was observed between TE and TW. Insignificant positive correlation coefficients also occurred between EW and DWS, DAS, D, and TW. DWS, DAS and D were closely and positively associated; each was insignificantly negatively correlated with TE.

Relationships of yield efficiency on the basis of leaf area at silking (YE_L), harvest index (HI), and leaf area duration after silking (D) with translocation efficiency (TE) and yield efficiency on the basis of leaf area duration (YE_D) are shown in Table 5. Consistent positive correlation coefficients occurred among YE_L , HI, YE_D and TE. They were highly significant except between YE_L and TE; the significance was at the 0.10 probability level. Leaf area duration (D) varied negatively, but insignificantly, with TE and YE_D . Also, YE_L , HI, and YE_D each varied negatively, but insignificantly, with the vegetative variables, TW, DWS, and DAS.

Longer growth duration and longer leaf area duration accounted for larger total plant dry weight at maturity as well as for dry matter produced after silking as reported by Yamaguchi (11). However, leaf area duration after silking, total plant dry weight at silking, and dry matter produced after silking had little effect on ear dry weight. Tanaka and Yamaguchi (10) and Yamaguchi (11) reported leaf area duration,

Table 4. Relationships of total dry weight at silking (DWS), dry weight production after silking (DAS), dry weight production efficiency after silking (DWE), translocation efficiency (TE), and leaf area duration (D) with tassel dry weight (TW) and ear dry weight (EW) of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

| Variables | TW | EW |
|-----------|-------------|-------|
| | -----T----- | |
| DWS | 0.933** | 0.270 |
| DAS | 0.826* | 0.384 |
| DWE | 0.129 | 0.207 |
| TE | -0.711 | 0.022 |
| D | 0.972** | 0.385 |
| TW | 1.000** | 0.447 |

* = r significant at 0.05 probability level;

** = r significant at 0.01 probability level.

Table 5. Relationships of yield efficiency on the basis of leaf area at silking (YE_L) harvest index (HI), and leaf area duration (D) with translocation efficiency (TE) and yield efficiency on the basis of leaf area duration (YE_D) of synthetic hybrids and original populations at Manhattan, Kansas, during 1975.

| Variables | TE | YE_D |
|-----------|-------------|---------|
| | -----r----- | |
| YE_L | 0.787+ | 0.953** |
| HI | 0.960** | 0.985** |
| D | -0.789+ | -0.673 |
| YE_D | 0.9114** | 1.000** |

+ = r significant at 0.10 probability level;

* = r significant at 0.05 probability level;

** = r significant at 0.01 probability level.

total plant dry weight at silking, and dry matter produced after silking was positively associated with grain yield. That occurred in this study only when the mean of all synthetics was compared with the mean of all original populations.

Uniformity among entries in the source of assimilates (either current photosynthesis during grain filling or translocation of photosynthates prior to and during grain filling) would result in an association of leaf area duration, total plant dry weight at silking, and dry matter produced after silking with ear dry weight. Lack of uniformity, on the other hand, would cause no or poor correlation.

Translocation efficiency did not affect ear dry weight consistently for the reasons given above: lack of uniformity among entries in the source of assimilates for ear growth.

Larger tassel size, total plant dry weight at silking, dry weight produced after silking, and leaf area duration appeared to be good indicators of excessive vegetative growth. They were negatively associated with translocation efficiency. Yield efficiency expressed on the basis of leaf area at silking or leaf area duration and harvest index were good indicators of translocation efficiency.

Two mechanisms, larger leaf area or yield efficiency, were probably responsible for higher grain yields as observed in previous experiments (8). The concept of increasing grain yield by adjusting planting densities is based on the assumption that the source of assimilates, not the kernel sink, is the limiting factor for higher grain yield. Storage of assimilates produced after silking in vegetative parts at silking is detrimental to the potential grain yield. Reported

positive association of small tassel size (2), yield efficiency (2, 10), and small plant vegetative size (11) with density tolerance was probably related to translocation efficiency.

The effect of the combined selection criteria, yield per plant (YP) and yield per unit leaf area at silking (YE), varied with populations. These selection criteria apparently established an equilibrium between the source and sink in KDS and Mex-Mix. The equilibrium between source and sink in KDS was at the expense of translocation efficiency; selecting for YP and YE simultaneously appeared to be inappropriate for promoting density responsiveness in most situations (8). Consequently, YE alone would be the most appropriate selection criterion for density tolerance.

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PHYSIOLOGICAL RESPONSES OF THREE
MAIZE (Zea Mays L.) POPULATIONS TO
SELECTION FOR HIGH GRAIN YIELDS

by

Myanguila Muleba

B.S.A., National University of Zaire, 1967

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY

Manhattan, Kansas

1976

Rapid methods of estimating leaf area and yield efficiency and relationships among some physiological traits associated with high grain yields were determined in three open-pollinated maize populations [Kansas Drought Synthetic (KDS), Amarillo-Bajio, and Mex-Mix]. Selections were made among 100 families in each population at Manhattan, Kansas and Tlaltizapan, Mexico during 1974. Synthetic hybrids from selections based on combined criteria of yield per plant (YP) and yield per unit leaf area (YE) were made in each population for specific adaptation and for wide adaptation. All selections were compared to their respective original populations for grain yields and physiological responses during 1975. Growth analysis studies, comparing the Manhattan specific adaptation selections to their respective original populations, were conducted at Manhattan during 1975.

Total plant leaf area (LAp) and leaf area (LA) of each of the thirteen top plant leaves were positively and highly significantly correlated. Highest correlation coefficients with LAp occurred with leaf 8 ($r = .94$) in KDS, leaf 9 ($r = .84$) in Amarillo-Bajio, and leaf 7 ($r = .72$) in Mex-Mix. Several combinations of areas of two or three leaves gave a better prediction of LAp in regression analysis studies. Eight leaf area factors (LAF) based on a single leaf (7, 8, and 9) on the sum of two or three leaves (2+9, 2+11, 7+11, 7+11+2, and 11+9+2) from one replication provided equal or better estimations of LAp in a second replication. There was no advantage of using more than one leaf in computation LAF's. Yield efficiency based on area of the single leaves or the sum of two or three leaves used in the computation of LAF

varied closely and highly significantly with YE based on LAp in all three populations. The coefficient of variation remained nearly constant in each population regardless of how YE was calculated.

Photosynthetic sources were apparently not the limiting factors for higher grain yield, but kernel number (KN) was. Higher yielding genotypes had two mechanisms for high yields: a large leaf area index (LAI) for intercepting more incoming light, or a high efficiency of grain production per unit leaf area. The latter mechanism was suggested by positive association of YP with YE, KN with YP and YE, and LAI with YP, and by negative association of LAI with YE.

Longer growth duration and leaf area duration accounted for larger total plant dry weight at maturity. Plant vegetative characteristics--total dry weight at silking, dry matter production after silking, tassel size, and leaf area duration (D)--were closely associated with each other. Large values for these measurements indicated excessive vegetative growth; they were negatively correlated with translocation efficiency (TE), YE, and harvest index (HI).

Yield efficiency based on LA at silking or D and HI were closely associated. They were good indicators of translocation efficiency because they were closely associated with TE. The effect of selection for YP and YE depended on the weight of YP and YE in the selection criterion. Positive and concurrent responses for both YP and YE would require close association between YP and YE and similar signs for correlation coefficients of LAI with YP and YE.