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Growth and yield of highland maize in Mexico

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SUMMARY

The growth and yield of five highland varieties of tropical maize were studied. Grain yields were between 4·7 and 8·8 t/ha. Crop growth rates (C) increased to a maximum of between 25 and 35 g/m^2/day at silking and then declined. Grain growth rates (maximum 21 g/m^2/day) exceeded current C during most of the grain-filling period.

After silking, when C exceeded grain growth rate, dry matter accumulated in the stem and husk, resulting in an increase of from 200 to 600 g/m^2. Later, as grain growth rate increased and exceeded current C, some of this accumulated material was incorporated into the grain, and stem weight decreased. A comparison of the dry weight changes after flowering in these varieties with those reported for a hybrid that yielded 12 t grain/ha indicates that the smaller yield of the Mexican varieties was associated with smaller grain growth rates and the incorporation into the grain of a smaller fraction of the dry weight produced after flowering. These results suggest that the capacity of the grain 'sink' to utilize assimilates limited yields in the tropical varieties.

INTRODUCTION

Even under good management, the grain yields of maize in tropical latitudes are usually smaller than the yields obtained in the maize producing areas of the United States.

Studies have been carried out during the past 3 years at the International Maize and Wheat Improvement Centre (CIMMYT) in Mexico to examine the growth and yield of tropical lowland and highland varieties of maize, with the object of determining what factors currently limit yield and what might be done to overcome these limitations.

In the experiment described in this paper, five tropical highland varieties of maize were investigated. Their growth and grain yield are compared with the growth and yield of a high yielding hybrid (SR 52) grown at a similar latitude, but south of the equator (18° S) at Salisbury, Rhodesia, as reported by Allison (1969).

METHODS

Plant material

The five highland varieties studied were: C.I.P.A., which is an early, inter-racial, highland composite; Hidalgo 8 × Mexico Group 10, a tall, late Chalqueño variety; Zacatecas, 58, which is a very early, short variety; Criollo Baraza, an early variety used locally in the Toluca valley in Mexico; and H 28, which is a locally bred (I.N.I.A.) hybrid.

Field experiment

The experiment was carried out at CIMMYT's research station at El Batán, Mexico (altitude 2250 m, 19° 31′ N, 98° 50′ W). The five varieties were sown on 15 April 1972 at 50000, 100000 and 150000 plants/ha, in a split-plot layout with varieties as mainplots and plant densities as subplots. The treatments were replicated four times.

The soil was well fertilized and the experiment was irrigated whenever necessary to supplement rainfall.

Figure 1 shows the mean values for 10-day periods for solar radiation, maximum and minimum temperatures, experienced at El Batán in 1972.

Where irrigation is available, as at El Batán, the growing season for maize is limited by frosts to the months from April to October.

Measurements of leaf area and dry weight

A randomly selected sample of plants was harvested at 7-day intervals, from 53 days after sowing. At densities of 50000 plants/ha the samples consisted of a row of ten plants at first, but later, as the plants grew, the number was reduced to six. At 100000 and 150000 plants/ha the samples consisted of ten plants throughout.

Plants were harvested together with the part of the roots which could be recovered easily with a garden fork.

Shoots were divided into stem (including sheaths),

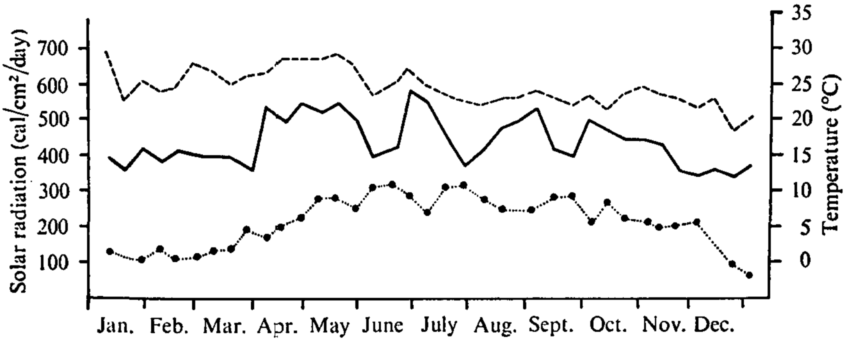

Fig. 1. Temperature and solar radiation. El Batán, Mexico, 1972 (10-day means; 2250 m altitude, 19° 31′ N, 98° 50′ W). --, Maximum temperature; ——, solar radiation; ●....●, minimum temperature.

green laminae, dry leaves and root. Green laminae were separated by detaching them at their junction with the sheath or, if they were not fully expanded, at a level where they emerged from the sheath of the uppermost expanded leaf. After flowering, the developing ear was divided into husk, cob and grain. The separate parts were then weighed and their dry weight estimated from the dry weight of subsamples. The stem and husks were chopped finely before taking the subsample for drying.

Laminae area was estimated from the ratio of area to dry weight of a subsample and the total laminae dry weight. The area of the laminae subsample was measured on a photometer.

Leaf area and dry weight/unit area of land were calculated from the leaf area and dry weight of samples and from counts at 2-week intervals of the number of plants in a known area.

Crop growth: methods of analysis

To describe the changes in dry weight/unit ground area (W) and of leaf area index (L) with time (t), a cubic polynomial was fitted to the observed values of W and L in the manner described by Allison (1969) and also to the logarithms of W and L in the manner described by Hughes & Freeman (1967). The advantages of a regression form of analysis of this kind have been discussed by Radford (1967).

The two attributes of growth discussed in this paper namely crop growth rate (C) and net-assimilation rate (E) can be derived from either of these forms of curves as:

$$\text{crop growth rate} = \frac{\delta W}{\delta t},$$

$$\text{net assimilation rate} = \frac{1}{L}\frac{\delta W}{\delta t}.$$

To test whether the model was adequate, equations were computed for fitting the model to the means of W and L and to the means of the logarithms of W and L. A comparison was then made of the residual variance between harvests and the variance between replicates (within harvests). In all cases the variance between replicates was negligible. The linear and quadratic components accounted for more than 95% of the variation in W and ln W with time: the quadratic component accounted for most of the variation in L and ln L with time.

The next step was to compute the equations for fitting the model to the values of W and L and of ln W and ln L for each plot separately. Values for the crop growth rate and net assimilation rate were derived in the manner described by Allison (1969) and by Hughes & Freeman (1967) for each harvest, for each plot. The standard error of the means of a derived variate at each harvest was obtained from an ordinary analysis of variance of the estimates for the individual plots.

Since the variance of W increases as W increases, it is preferable to use the logarithmic transformation for the regression analysis (Radford, 1967). The analysis for these experiments indicated that except for the first few and the last few harvests when the restrictions of the model give rise to unreliable estimates, the transformed data gave better estimates of the derived values of C and E than the untransformed data. The values of C and E were therefore obtained from the regression of ln W and ln L with time. Untransformed values provide a simpler representation of changes in W and L with time and have therefore been used for this purpose in the diagrams that follow.

To compare the growth and yield of the five varieties studied in this experiment with the hybrid SR 52, similar curves were fitted to the mean values of W and L reported by Allison (1969).

RESULTS

Development

Development data for the five varieties studied are shown in Table 1.

Table 1. *Development data for five highland varieties of maize (days from sowing)*

Variety	Initiation of apical inflorescence	Emergence of silks	Physiological maturity
C.I.P.A.	20	81	162
Hidalgo 8	23	95	179
Zacatecas 58	19	65	140
Criollo Baraza	18	70	141
H 28	28	85	170

Table 2. *Grain yield and yield components of highland maize El Batán* 1972

Variety	No. of plants/m²		Weight of 1000 grains (g)		No. of grains/m²			Grain yield (g/m²)		
	Mainstems	Tillers	Mainstems	Tillers	Mainstems	Tillers	Total	Mainstems	Tillers	Total
C.I.P.A.	4·6	5·7	307	271	1821	533	2354	559	144	704
	8·9	4·7	288	238	2906	157	3063	837	37	874
Hidalgo 8	4·5	4·5	260	201	2550	485	3035	663	98	761
Zacatecas 58	4·6	5·1	285	258	1500	403	1903	427	104	531
	9·4	2·8	268	241	2522	108	2630	676	26	703
	14·0	1·2	254	289	2987	30	3017	757	9	766
Criollo Baraza	4·4	4·8	257	196	1742	127	1869	448	25	473
H 28	4·6	4·5	329	262	1901	287	2188	625	75	700
	9·7	1·9	285	257	2938	186	3124	838	48	886
	13·7	1·7	253	204	2906	326	3232	734	67	802
SR 52*	7·4	—	—	—	—	—	—	—	—	1200

* Data source: Allison (1969).

Zacatecas 58 which was the earliest of the five varieties (65 days to silk emergence) produced 13 or 14 leaves; Hidalgo 8, which was the latest variety (95 days to silk emergence), produced from 19–24 leaves on the main shoot.

Like other highland varieties of maize, all produced tillers. At the lowest plant density there was usually one tiller per plant at harvest in all varieties (Table 2). As density increased the number of tillers that survived decreased to less than one for every ten plants at 150000 plants/ha.

Grain yield

The grain yields and a summary of the components of yield are shown in Table 2. Three of the varieties lodged at high densities; C.I.P.A. lodged at 150000 plants/ha while Hidalgo 8 and Criollo Baraza lodged at both the high densities. No attempt was made to analyse the growth or yield of crops that lodged so these treatments have been omitted from Table 2 and from all subsequent tables and graphs.

Of the five varieties, C.I.P.A. and H 28 gave the largest grain yields, (8·8 t/ha) while all other treatments except for the two earliest varieties, Zacatecas 58 and Criollo Baraza, grown at the low density (5·3 and 4·7 t/ha respectively), yielded more than 7 t/ha. These yields are small compared with the 12 t/ha produced by SR 52. Except when the varieties lodged, grain yield increased with increase in plant density.

Differences in yield between varieties and plant density were examined in terms of the components of yield, namely the number of ears/plant (which with plant density determines the number of ears/unit area), the number of grains/ear and the size of the grain. Yield was proportional to the number of grains/m². Although grain size usually decreased with increased density, the effect on yield was small compared with differences in the number of grains. Thus the increase in grain yield with increase in plant density was accounted for mainly by an increase in the number of grains/m² (Table 2).

The ears on the main stems contributed 80% or more of the total grain yield, even at the lowest plant density, which had the greatest number of tillers. At the higher density tillers accounted for between 1 and 8% of the grain yield.

Crop dry weight

The changes in dry weight of the crops and the corresponding changes in the dry weight of grain are shown in Fig. 2(*a*).

Dry weight produced by the two early varieties, Zacatecas 58 and Criollo Baraza was less than that of the other, later varieties (at 50000 plants/ha dry

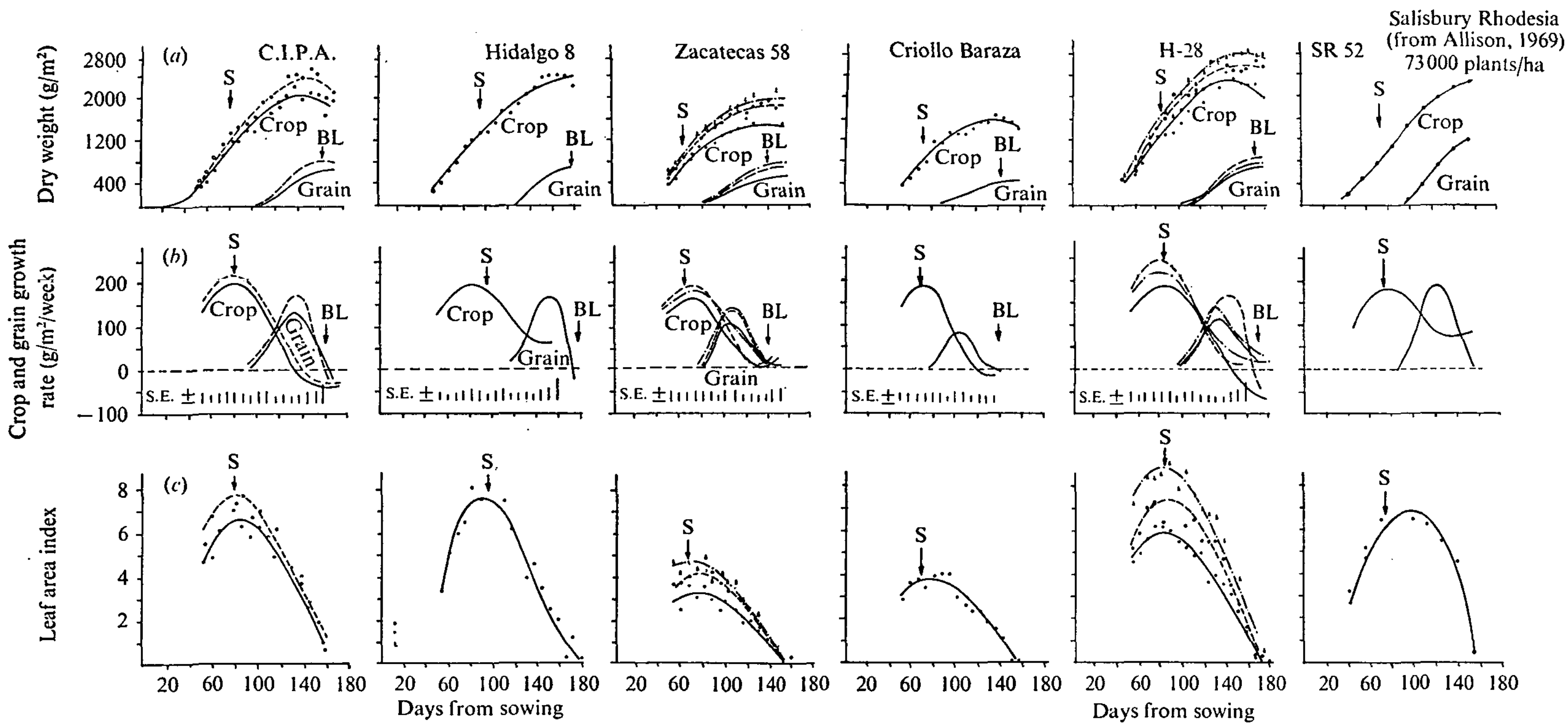

Fig. 2. (*a*) Dry weights of crop and grain. ●—●, 50000; ○—○, 100000; △-·-△, 150000 plants/ha. (*b*) Growth rates of crop and grain, ——, 50000; ----, 100000; —·—, 150000 plants/ha. (*c*) Leaf area index, ●—●, 50000; ○---○, 100000; △—·—△, 150000 plants/ha. S and BL indicate date of silking and date of formation of black layer (physiological maturity).

weight yields were 14 and 24 t/ha for Zacatecas and Hidalgo 8 respectively). The dry weight produced by three of the Mexican varieties was similar to that of SR 52, although, as shown earlier, grain yields differed. The harvest index (ratio of grain yield: total dry weight) of SR 52 was 0·53 and of the Mexican varieties was between 0·29 and 0·40. Provided crops did not lodge, dry weight increased with increase in plant density.

The total dry weight of a crop depends on the duration of growth and on the crop growth rate. Thus the smaller total dry weight of the two early varieties was accounted for partly by their shorter period of growth: 140 days compared with 163–179 days, to physiological maturity. However, there were also distinct differences in crop growth rate between varieties and densities, as shown in Fig. 2(*b*). In all varieties crop growth rate increased to a maximum at silking and then declined. In the two early varieties, it reached a maximum about 10 days earlier and declined to a near zero value sooner (120–140 days after sowing) than in the late varieties (140–170 days after sowing).

Except for Zacatecas 58 at the lowest plant density, in which the crop growth rate was smallest, the maximum crop growth rates of the varieties were similar at corresponding plant densities and varied between 175 and 250 g/m^2/week. Plant density had no significant effect on time to flowering or maturity so that the increase in dry weight with increase in plant density in the varieties C.I.P.A., Zacatecas and H 28 was accounted for mainly by differences in crop growth rate.

The curves showing the grain growth rates in Fig. 2(*b*) were derived from cubic polynomials fitted to the logarithms of the grain weights, in the same way that crop growth rates were derived from crop dry weight. In all the Mexican varieties crop growth rates were already declining rapidly when grain growth commenced. Without exception, as crop growth declined and grain growth increased toward a maximum, grain growth rates exceeded crop growth rates. The maximum grain growth rates were reached either a little before or as crop growth rates reached near zero values.

There are two possible explanations for this pattern of change in dry weight: first, it is possible that a large part of the grain dry matter is derived from assimilates which accumulate in plant parts other than grain and are then translocated to the grain. Alternatively, if as reported by Allison & Watson (1966) and by Palmer, Heichel & Musgrave (1973), the dry matter that fills the grain is derived from current assimilation, then presumably the large loss in weight from other parts of the plant, mainly the stems, represents respiration losses that are not replaced by current assimilation. The pattern observed is probably a combination of these two, with both current assimilation and re-translocation contributing to grain weight. No direct measurements of movement of assimilate were made in this study so that it is not possible to determine with certainty the extent to which re-translocation accounts for the changes in weight observed.

However, the form of the growth curves suggest a division of the growth after flowering into three periods which makes it possible to estimate the probable magnitude of the storage and re-translocation involved. The three periods are:

(1) From silking to the beginning of dry weight accumulation in the grain.

(2) From the beginning of dry weight accumulation in the grain until the grain growth rate exceeds crop growth rate (Fig. 2*b*).

(3) From the end of period 2 until harvest.

After flowering there is little further structural growth so that the increase in crop dry weight in the first period, before dry weight increase in the grain has begun, probably represents storage (ΔW_1, in Fig. 3). Most of the increase in weight at this time is in the stems and husks (stover).

The increase in crop dry weight during the second period (ΔW_2) exceeds the increase in grain dry weight (Δw_2) and the difference ($\Delta W_2 - \Delta w_2$) is an estimate of probable further storage in stover. The total storage during the first two periods is estimated as $\Delta W_1 + (\Delta W_2 - \Delta w_2)$ in Fig. 3.

During the third period, the increase in grain weight (Δw_3) is larger than the increase in crop dry weight (ΔW_3) and the difference ($\Delta w_3 - \Delta W_3$) also shown in Fig. 3, provides an estimate of the probable contribution to grain weight from material that is re-translocated. Clearly losses in crop dry weight as observed for example in C.I.P.A. and H 28 cannot represent translocation and where such losses occurred the maximum dry weight attained was used to estimate ΔW_3. From an analysis of this kind it is evident that there is probably a large amount of storage during the first period, immediately after flowering in all the materials. The values of ΔW_1 were between 250 and 400 g/m^2 (Fig. 3).

In the second period the amounts stored ($\Delta W_2 - \Delta w^2$) were usually smaller, though not in H 28. The increase in grain weight (Δw_2) accounted for less than 40% of the increase in dry weight (ΔW_2) in the Mexican varieties and 77% in SR 52. This difference was associated with a more rapid increase in grain growth rate in the Rhodesian hybrid SR 52.

The combined duration of the first two periods was similar in all varieties, from 30 days for Zacatecas and Criollo Baraza to 39 days for H 28. This is perhaps surprising considering that there was a difference between varieties of 30 days in

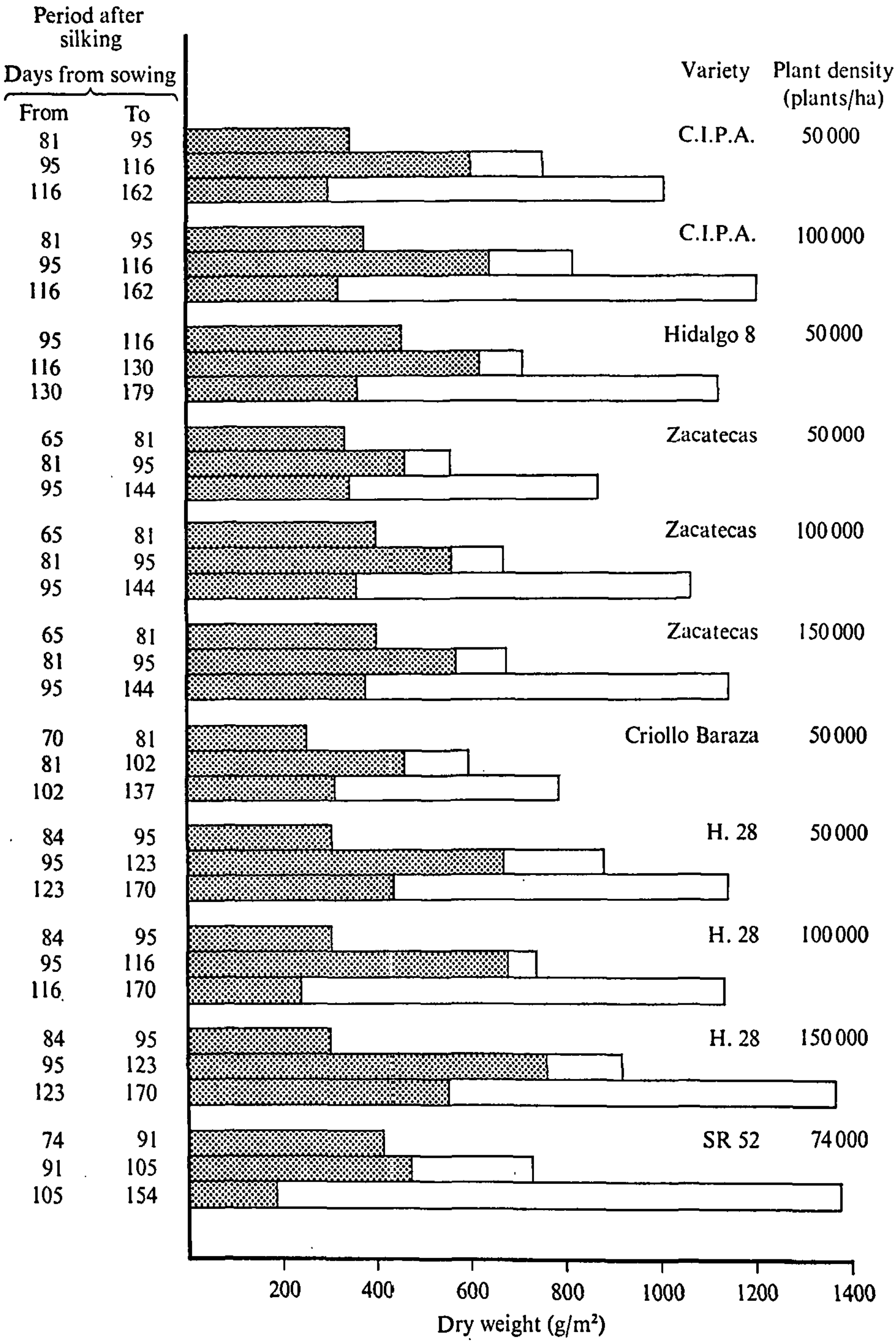

Fig. 3. For legend see opposite.

Table 3. *Leaf area duration after flowering (D) and ratio (G) of grain: leaf area duration after flowering for highland maize*

	Plant density (plants/ha)	Leaf area duration (*D*) (weeks)	Grain:leaf ratio (*G*) ($g/m^2/week$)
C.I.P.A.	50000	54·7	12·9
	100000	60·0	14·6
Hidalgo 8	50000	51·0	14·9
Zacatecas 58	50000	27·5	19·3
	100000	34·6	20·3
	150000	38·3	20·0
Criollo Baraza	50000	32·5	14·6
H 28	50000	48·9	14·3
	100000	60·8	14·6
	150000	64·3	12·5
SR 52	74000	54·3	22·1

time to flowering. During this first 30 or more days after flowering storage other than grain amounted to between 4·5 and 7·6 t/ha.

In the third period the increase in grain weight (Δw_3) exceeded the increase in total dry weight by between 119 and 400 g/m^2. The difference provides an estimate of the probable amount of re-translocation to the grain, and suggests that the fraction of previously stored material that is utilized in this way varied from about 30% in Zacatecas 58 for example to more than 60% in SR 52 and in H 28 at the intermediate plant density. The increase in total dry weight in this period was also significantly larger in SR 52 than in the other varieties.

Thus the Rhodesian hybrid differed from the Mexican varieties in three main respects: it exhibited a much more rapid increase in grain growth rate once grain growth had started and thus incorporated into the grain relatively more of the current assimilate in period 2; it maintained crop growth rate for longer, well into the period of formation of grain dry weight; a comparatively large fraction of the material that accumulated in other parts of the plant after flowering was eventually incorporated into the grain.

These three factors accounted for the much larger grain yield of the hybrid.

Leaf area index and net assimilation rate

The variation in crop growth rate (*C*) is dependent on the variation in leaf area index (*L*) and net assimilation rate (*E*), since $C = L \times E$.

In all varieties the leaf area index increased to a maximum at flowering and then declined (Fig. 2*c*). The most conspicuous difference in leaf area index, as with crop dry weight, was provided by the contrast between the two early varieties and the other three. Following the example given earlier for crop dry weight, the maximum value of *L* for Hidalgo 8

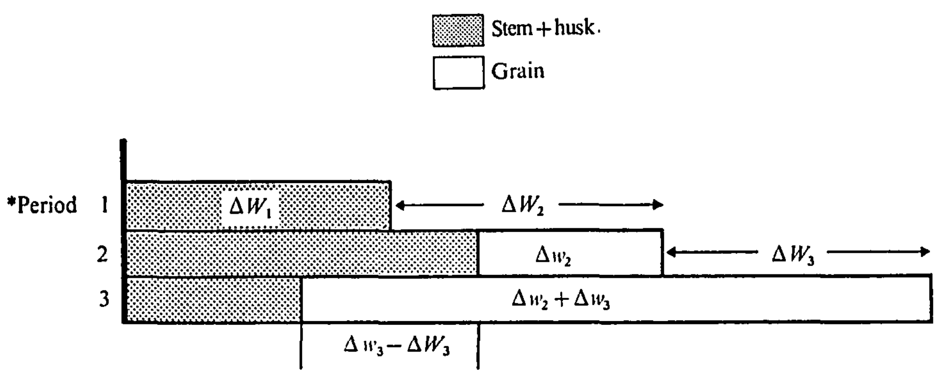

Fig. 3. The accumulation and distribution of dry weight in maize during three periods after silking.* Key to components of change (see text).

at 50000 plants/ha was 7·5; the corresponding value for Zacatecas 58 was 3.

Hidalgo 8 and Criollo Baraza lodged at densities greater than 50000 plants/ha, but in the other three varieties leaf area index increased with plant density. The largest leaf area index at flowering ($L =$ 8·8) was produced by H 28 at 150000 plants/ha.

The rates of dry-weight production per unit leaf area (net assimilation rate) were high at silking. This combined with the large leaf areas accounted for the peak growth rates observed.

The rapid decline in crop growth rates after silking was related to the simultaneous and rapid decline in leaf area and net assimilation rate.

The production of dry weight after silking is related to the amount and duration of leaf area after silking (D) and to the efficiency of the leaf area. Values of D, calculated as the integral of leaf area over time, are shown in Table 3. The two early varieties, Zacatecas 58 and Criollo Baraza had much smaller values of D than other varieties, but Zacatecas produced more dry weight per unit of leaf area duration than the later varieties.

The ratio G (grain yield: D) is a measure of the efficiency of the leaf area that persists after flowering for grain production. It can be seen from the values in Table 3 that the hybrid SR 52 produced much more grain per unit of leaf area duration than the Mexican varieties. Zacatecas 58, at all three plant densities was also more efficient in this respect than other varieties and the values of G for Zacatecas were only slightly smaller than those of SR 52 even though in Zacatecas stored material contributed less to grain yield than it did in SR 52.

DISCUSSION

The smaller grain yields of the five tropical varieties when compared with the Rhodesian hybrid SR 52, were associated with smaller grain growth rates and a larger accumulation of dry weight after flowering in the stover.

Allison & Watson (1966) have shown that when the grain 'sink' is removed by preventing pollination, the dry matter that would have passed to the grain accumulates in the stover. Also that when the 'source' of assimilate is restricted by removing leaves, stem weight decreases as previously stored dry matter moves to the grain.

The pattern of growth and dry weight distribution observed in the tropical varieties described, strongly suggests that the capacity of the grain sink limits grain production. The accumulation of dry weight in stover immediately after silking and before grain growth started, was similar in all the varieties. The initial rate of grain growth was much more rapid in SR 52 than in the Mexican varieties. This was associated with higher crop growth rates and less accumulation of dry weight in stover. In contrast the slower increase in grain growth rate in the Mexican varieties was accompanied by further large accumulations of dry weight in stover, and rapid declines in C which were not explained fully by changes in leaf area index. Net assimilation rates also decreased. This may have been due to a decrease in photosynthesis, an increase in respiration, or both. Net photosynthesis decreases with age of leaves (Friend, 1966) and may also be influenced by the demand for assimilates (Moss, 1962). The reduction in E may indicate that photosynthesis had ceased or, more probably, that respiration losses associated with re-translocation to the grain, combined with respiration of previously stored material that could not be accommodated in the grain, exceeded current photosynthesis. Thus with the exception of Hidalgo 8 in the Mexican varieties, dry weights reached a maximum and then declined, even before grain growth was complete.

The total dry weights of Hidalgo 8 and H 28 were similar to those of SR 52 and it seems that, but for the limiting capacity of the grain sink, these varieties could have produced more yield.

There are several ways in which the shortcomings of the tropical varieties described might be overcome. First, if the pattern of growth and distribution observed in SR 52 is characteristic of maize grown in the United States (from where it was derived), is this heritable and can it be introduced into tropical materials? The problem with materials from the United States in the past has been their susceptibility to disease and insect damage when grown in a tropical environment.

A second course is to explore more fully the potential for improving the yield of early tropical varieties. The dry weight produced before flowering was similar in SR 52 and the two early Mexican varieties (about 800 g/m^2); it was much larger (1200–1600 g/m^2) in the other varieties. Much of this dry weight accumulation is associated with a very rapid elongation of the stems which occurs at the time the lateral inflorescences are developing. The expanding internodes provide a large sink for assimilates and it seems probable that their growth may compete with and limit the development of the structures where later, grain growth will occur. In early varieties, with smaller stems, this internal competition may be less severe.

A further possibility is to examine whether the observed limitations can be overcome by selection within the highland, tropical varieties. Before this can be attempted a better understanding is needed of the factors that determine eventual grain sink size.

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