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THE RELATIONSHIP BETWEEN YIELD AND QUANTITATIVE SHOOT MORPHOLOGY AND THE DEVELOPMENT OF INDIVIDUAL LEAVES IN SIX TRINIDAD CASSAVA *(MANIHOT ESCULENTA* CRANTZ*)* CULTIVARS

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INTRODUCTION

Cassava is a major starch producer in the third world, particularly in the wet tropics, having an estimated annual world production of 104.9 million metric tons (M.T.) (FAO 1974). Estimated production in the Commonwealth Caribbean is 50,000 M. T. all of which is used for direct human consumption. But with cassava's many uses (Neusbaum, 1970) such as a flour substitute (Chatelenat, 1970), in animal feeds and in starch-based industries (McCann, 1976) there is great scope for increased production to replace traditional import crop commodities, e.g; wheat flour, maize feeds, and starch.

Caribbean cassava productivities are low, particularly for small production zones, except for Barbados (Table 1) and well below the yield potential of the species estimated at 66-90 ton. $ha^{-1}.yr.^{-1}$ by Cock (1974). The main reasons for low productivities include in efficient agronomic techniques and low yielding local cultivars. Therefore, there is need to identify or to synthesize new high yield cultivars suitable for cultivation in different Caribbean ecosystems. However, since random breeding from both new and existing cultivars is time consuming and wasteful of genetic material (Donald, 1962), it would be better to establish suitable plant ideotypes and to select cultivars with the required characteristics from segregating populations, for further hybridization programmes (Donald, 1968).

The existence of characteristics which affected yield production in crops was discussed by Donald (1968), Wilson (1974) and other workers. And there appeared to be two main types of characteristics : Firstly, those constraints in the crop/soil environment which limited yield development of a crop but did not affect the yield of the species, i.e. soil type, nutrition etc. Secondly, those physiological or morphological characteristics produced by the plant genotype which determined yield potential of the species, i.e. leaf area, yield components etc. There is a need to identify both the constraints and determinants of yield for maximum crop productivity.

In an on going study, we have analysed the growth of six local cassava cultivars in order to identify morphological and physiological yield determinants and their interrelationships with final yield. Quantitative morphological data on the mature plants were presented at the Fourth International Symposium for tropical root crops (Holmes & Wilson, 1976). In this paper, interrelationships between quantitative shoot and leaf ontogeny and biological and economic yield in the same six cultivars are presented and discussed.

MATERIALS AND METHOTS

Six local (Trinidad collection) cassava cultivars were grown in 1975, as previously described by Holmes and Wilson (1976). The cultivars were selected from local farmers ploits and were considered to be high yielding and "sweet". There were four broad, leaf-lobed cultivars, Whitestick I and II, Redstick and Maracas Blackstick, and two narrow, leaf-lobed cultivars, Around the World and Pie Pip.

At regular intervals during their growth, parameters of shoot morphology, i.e. number of branches, nodes, leaves and leaf scars respectively were recorded for 15 single shoot plants per cultivar. Individual leaf development and duration were also recorded for leaves emerging at 9, 14, 21 and 30 weeks after planting. At each period, the three smallest leaves per plant were identified and tagged and their petiole length, mid-lobe length and breadth, lobe number and stem internode lengths until maximum leaf size was achieved. Leaf area was calculated from linear leaf dimensions using the leaf rectangular area formula (Spencer, 1962). Average leaf area durations were computed from the area beneath a leaf area development curve to 50% abscission.

All measured data were subsequently analysed on the computer by Analysis of Variance using the subsample technique of Steel and Torrie (1962) with a Caribbean Agricultural Research and Development Institute's (CARDI) Computer Library Programme. Differences between treatment means were tested with Duncan's Multiple Range Test at p = 0.05 and p = 0.1 levels.

Table 1 - Cassava production and productivity in the Commonwealth Caribbean

Country	Production (ton x 10^3)	Productivity (ton/ha)
Barbados	1	26.7
Guyana	14	12.0
Jamaica	15	2.6
St. Lucia	15	
Trinidad & Tobago	5	9.0
Totals	50	12.6

RESULTS

Dry matter production and distribution, quantitative shoot morphology and economic yield data taken after 46 weeks of growth was presented by Holmes & Wilson (1976). From this analysis it was possible to identify three cultivar types on the basis of their biological and economic yields and harbest indices (Table 2). Close correlations between biological yield and parameters of shoot morphology were established (Table 3) within each cultivar. It was also proposed that excessive shoot development was linked to low harvest indices and that there might be a physiological barrier to achievement of hith harvest indices and high dry matter production in the same cultivar. Therefore, studies of the development patterns in the shoot and individual leaf were made to further elucidate interrelationships between these parameters of growth and yield in the six cultivars. The study was divided into two sections :

(1) Quantitative shoot ontogeny
(2) Quantitative leaf ontogeny

Table 2 - Classification of six cassava cultivars on bases of dry matter production and distribution and economic yield.

YIELD TYPES			CULTIVARS
A	High Dry Matter Production (30369 $g.p.^{-1}$ - 2997 $g.p.^{-1}$) Low Harvest Index (35.6 - 29.4)	High Economic Yield 2660 $g.p.^{-1}$ 2327 $g.p.^{-1}$	Whitestick I Whitestick II Redstick
B	Low Dry Matter Production (1885 $g.p.^{-1}$) High Harvest Index (52.5)	High Economic yield 2467 $g.p.^{-1}$	Maracas Black-stick
C	Low Dry Matter Production (1664 $g.p.^{-1}$ - 1424 $g.p.^{-1}$) Low Harvest Index 36 - 25	Low Economic Yield (1383 - 1191 $g.p.^{-1}$)	Around the World Pie Pip

1°/ Quantitative Shoot Ontogeny

Total leaf production was high in all cultivars (1231 N.P.$^{-1*}$-974 N.P.$^{-1}$), except Maracas Blackstick (664 N.P.$^{-1}$) after 46 weeks of growth (Fig. 1). Rates of node production were low in all cultivars up to 160 days (ave. rate 1.01 N.P.$^{-1}$) but differences between extreme cultivars were apparent and significant (p = 0.05). After 160 days, the average rate of node production in all cultivars was higher (5.10 N.P.$^{-1}$ dy.$^{-1}$). In this latter period, there were also significant differences between the low rate of node production in Maracas Blackstick (3.35 N.P.$^{-1}$ dy.$^{-1}$) and the other five cultivars (5.15 N.P.$^{-1}$ dy.$^{-1}$ - 7.10 N.P.$^{-1}$ dy.$^{-1}$).

There was proportionality between leaf production and leaf loss in all cultivars. Five cultivars had high (615 - 675 SP.P^{-1}) ≠ and one (Maracas Blackstck), low (318 S.P.$^{-1}$) scar number per plant after 46 weeks of growth. Leaf fall began approximately 90 days after planting and increased sharply only after 180 days. However there was a reduction in the rate of appearance of leaf scars at 160 to 180 days after planting which coincided with the onset of rapid leaf area production due to either a relative increase in node production or increased leaf duration or a combination of both. There were significant differences in the percentage leaf fall (p=0.1) between cultivars from 96 - 150 days after planting, but after 46 weeks of growth, when the percentage leaf fall ranged from 52 % - 60 %, these differences disappeared.

The pattern of leaf retention (Fig. 2) during development was similar to that for node production, there being five high leaf number cultivars (454 L. R.$^{-1}$ - 584 L.R.$^{-1}$)* and one low leaf number (Maracas Blackstick - 288 L.R.$^{-1}$) cultivar after 46 weeks of growth. These cultivar differences were significant at the p = 0.05 level As with node production there were two phases of development in leaf retention, the mean rate for all cultivars during the early period (0 - 166 days) was 0.65 L. R.$^{-1}$ dy.$^{-1}$ and in the later period of growth (166 - 325 days) 2.45 L.R.$^{-1}$ dy.$^{-1}$. There was a brief period during development from 110 - 150 days when there was no increase and in the case of Maracas Blackstick even a reduction in leaf numbers retained. This coincided with the periods of early high leaf loss and low rates of node production, thus demonstrating the close relationship between leaf number, retention and node production and loss within each cultivar. However, final differences in leaf number between cultivars were due to differences in rates of node production, since there were no consistent and significant cultivar differences in the percentage leaf loss.

Data for number of branches per plant and mean number of nodes per branch are presented in Fig. 3. No branches appeared until day 80, after which time were slow increases in branch number up to day 170 in all cultivars except Maracas Blackstick in which branch number remained relatively consistent. After this time, branch number per plant increased rapidly through formation of axillary and flowering branches. Around the World had the highest final branch number (34.7 B.P.$^{-1}$).

In general, the high leaf number cultivars also had the highest branch numbers as the number of nodes per branch was similar in all cultivars, except in whitestick I, which produced some 19.2 branches and had a higher rate of leaf production per branch (58.8 N.B.$^{-1}$P^{-1}) than the remaining cultivars.

Since variations in the number of leaves retained per plant were related to relative rates of leaf production and leaf loss within each cultivar, and these rates were similar in all plants. Cultivar differences in leaf production became evident only after rapid branch production began. This pattern of leaf development was also observed in potato varieties (Das Gapta & Ghosh, 1973, and Taylor, 1973).

There were close correlations between leaf production and leaf retention to branch numbers in individual cultivars and over all cultivars during the period of rapid branch formation. This relationship was positive and highly significant (p = 0.001). Therefore, it was concluded that as the rates of leaf loss and leaf production

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Table 3 - Correlation coefficients between total dry matter and leaf number, node number, leaf area, in six cassava cultivars.

Cultivars	Node No./Plant	Leaf No./Plant	Leaf Area/Plant
	Corr. Coeff. (r)	(r)	(r)
1. Redstick	0.84 ***	0.90***	0.55*
2. WhitesticK II	0.59*	0.52*	0.61*
3. Whitestick I	0.69*	0.88***	0.80***
4. Maracas Blackstick	0.89***	0.83***	0.76***
5. Around the World	0.85***	0.91***	0.83***
6. Pie Pip	0.90***	0.76**	0.25 N.S.
All Varieties	0.64***	0.56***	0.69***

*** r = 0.001
** r = 0.01
* r = 0.05

N.S. - No Significance

TABLE 4. COMPARATIVE ANALYSIS OF QUANTITATIVE LEAF MORPHOLOGY IN SINGLE PLANTS OF SIX CASSAVA CULTIVARS

							Mean
	M.B.S.	White Stick II	White Stick I	Red Stick	A.T.W.	Pie Pip	
Petiole Length (cms) Means	22.4	19.9	19.5	18.7	14.95	13.8	18.2
SE ±			0.7177				
	A.T.W.	Pie Pip	M.B.S.	White Stick II	Red Stick	White Stick I	
Midlobe Length (cms) Means	17.75	16.4	13.2	11.78	11.76	11.32	13.7
SE ±			0.5134				
	M.B.S.	White Stick II	White Stick I	Red Stick	A.T.W.	Pie Pip	
Midlobe Breadth (cms) Means	3.55	3.48	3.34	3.13	1.36	1.32	2.7
SE ±			0.1188				
	M.B.S.	White Stick I	White Stick II	Red Stick	A.T.W.	Pie Pip	
Lamina Area (cm^2) Means	140.3	101.7	101.42	89	81	44	92.9
	Red Stick	White Stick II	M.B.S.	White Stick I	A.T.W.	Pie Pip	
Stem Internode Length Means	0.975	0.89	0.874	0.827	0.8189	0.771	0.859
SE ±			.0344				

Cultivar means joined by straight lines are not significantly different at p = 0.01 (Duncans Multiple Range Test).

TABLE 5 THE EFFECT OF PLANT AGE ON LEAF DURATION IN SINGLE SHOOT PLANTS OF SIX CASSAVA CULTIVARS

Time After Planting to Leaf Appearance (WKS)	INDIVIDUAL LEAF DURATION (Dys)									
	9 Time to 50% Leaf-fall	X Range (DYS)	14 Time 50% leaffall	X Range (DYS)	21	X	30	X	Mean	X
White Stick II	77	49.93	82.5	49-121	93	50-121	40	14-48	73.1	14-121
Around the World	74.5	48.93	96.5	57-127	100	55-123	43	18-50	78.5	18-127
Pie Pip	69.5	49.93	107.5	55-127	93	63-117	46	18-53	79.0	18-127
White Stick I	66.5	49.87	75	53-113	82	55-91	42	14-47	67.	14-113
Maracas Black Stick	58	46-70	60	53-93	82	50-104	47	21-55	61.7	39-99
Redstick	58	45-78	62	55-93	82	57-99	43	39-48	61.2	14-127
MEAN	67.25	45.93	80.6	53-127	88.6	50-123	43.5	14-50		

* Average time to 50% Leaf fall of 45 leaves per cultivar

per meristem were similar over all cultivars, manipulation of leaf numbers could be best achieved through change in branch number. A similar observation was made for Columbian cultivars (C.I.A.T. 1975).

2°/ Quantitative Leaf Ontogeny

Cultivar Effects on Quantitative Leaf Morphology

Parameters of quantitative leaf morphology for each cultivar over all time periods and leaves are presented in Table 4.

Three cultivar types were evident on the basis of leaf petiole length : long (Maracas Blackstick), intermediate (Whitestick II, I and Redstick) and short (Around the World and Pie Pip). Differences between cultivars were significant at p = 0.05 level, but those between Maracas Blackstick and Whitestick II and Redstick and Around the World were also significant at p = 0.1. Long (Around the World and Pie Pip), intermediate (Maracas Blackstick) and short (Whitestick I & II and Redstick) cultivar types were also identified on the basis of midlobe lengths. The former cultivars were significantly different from Maracas Blackstick which in turn had significantly longer leaf lobes than the remaining three broad-leaved cultivars. There were only small differences between leaf lobe widths amongst the four broad-leaved cultivars (3.13 - 3.55 cms.), but both narrow-leaved cultivars had significantly smaller (p = 0.1) widths (1.32 - 1.36 cms.) than the rest of the cultivars.

Because individual lamina areas were calculated in this instance from the cultivar means it was not possible to compute standard errors. However, individual leaves of Maracas Blackstick had 38 % greater lamina area than those in the cultivar with the next largest leaf (Whitestick II), and lamina area in Around the World was 10 % less than the smallest broad-leaved cultivar, (Redstick), which suggested significant differences might exist between the six cultivars on the basis of individual leaf size.

Stem internode lengths ranged from 0.975 to 0.771 cms. with Redstick having the longest internodes and Pie Pip the least.

Therefore, in respect of all parameters of leaf size and leaf display, the four broad-leaved cultivars, particularly Maracas Blackstick, were superior to the thin-leaved low yielding cultivars.

Effect of Time of Leaf Appearance

Fig. 4 shows the effect of time of leaf appearance on mean leaf development over all cultivars. All parameters were smallest after 9 weeks of growth particularly petiole length and lamina area. Petiole length remained constant in leaves formed after week 14, as did leaf midlobe breadth, but midlobe length increased through week 30 to result in similar increases of lamina area. However, the lamina area which was also affected by midlobe breadth size and leaf lobe number showed only a small increase from week 21 to 30. Leaf size in Columbian cultivars also varied with plant age but mean leaf area increased only until the 16th week after which it declined (C.I.A.T. 1975). This was not the case in the six cultivars studied here.

Leaf Duration and Leaf Area Duration

There was great variation in the duration of individual leaves within each cultivar, as well as a long period from the fall of the first to the last within each time period (Table 5). Over all times, Around the World (78.5 days) and Pie Pip (79.0 days) had marginally longer leaf durations than the other cultivars and Maracas Blackstick (61.7 days) and Redstick (61.2 days), the least. These differences would be most clearly discerned after 9 and 14 weeks of growth, particularly in the short leaf duration cultivars. Plant age and/or the environment at time of

TABLE 6. THE EFFECT OF PLANT AGE ON INDIVIDUAL LEAF AREA DURATION IN SINGLE SHOOT PLANT OF SIX CASSAVA CULTIVARS

	INDIVIDUAL LEAF AREA DURATION (cm^2 DAY)				
Plant Age At Leaf Emergence (WKS After planting)	9	14	21	30	Mean
CULTIVARS					
White Stick II	5167.0	9,250.0	13,020.0	2,327.0	7690
White Stick I	4150.0	9,530.0	10,610.0	2,800.0	6772.5
Red Stick	3361.0	6,216.0	9,399.0	6,140.0	6279
Maracas Black Stick	4452.0	7,045.0	12,510.0	5,933.0	7484.5
Around The World	3838.0	11,536.0	11,118.0	2,480.0	7243.0
Pie Pip	4268.0	10,550.0	4,809.0	1,825.0	5463
MEAN	4206	9,021	10,244.3	3,584.2	

* Calculated from area beneath line of an area u time plot for each Cultivar. Time to 50% leaf abscission. Area measured on a Hayasmi denro Co. Ltd. Leaf area meter. Type AAM-5

leaf appearance affected leaf appearance affected leaf duration, with the leaves formed at 21 and 14 weeks having the longest and those at 30 weeks the shortest duration.

Individual leaf area duration (Table 6) which was a combination of lamina area and leaf duration and was a measure of the effective leaf assimilatory period, varied considerably between cultivars over all time periods (5463 cm^2. dy. - 7690 cm^2 dy.) with Whitestick II having the greatest and Pie Pip the least values. Though statistical analysis was not possible, the cultivars could be separated into three leaf area duration types : long (7690 - 7243 cm^2.dy.), intermediate (6772 - 6279 cm^2 .dy.) and short (5463 cm^2 .dy.). As with leaf area, the leaves formed after 21 weeks had the longest leaf area durations (10,244.3 cm^2.dy.) and those at 30 weeks the least (3584.2 cm .dy.). However, the pattern varied between cultivars, with Around the World and Pie Pip having longest leaf area durations in leaves formed after 14 weeks rather than 21 weeks. Moreover, Maracas Blackstick and Redstick did nos show the large reductions in leaf area duration after 30 weeks evident in the other cultivars. The longer leaf area duration in Around the World was a consequence of the longer leaf duration, rather than higher leaf area. It is suggested that the small leaf size in Around the World and low leaf area duration in Pie Pip were both contributory factors to the low dry matter production in these cultivars.

DISCUSSION

The analysis of shoot growth confirmed the existence of high and low leaf area cultivars. It also emphasized importance of branch production for leaf production and retention, especially as there were no apparent genetic differences in the rate of leaf production per meristem and percentage leaf loss. High rates of leaf turnover were due to continuing leaf production associated with the perennial scrub habit of the cultivars, allied to short leaf duration of the leaves produced. High leaf production might also have hastened leaf fall due to mutual shading of the lower leaves.

The was evidence of genetic variation in the leaf duration and individual leaf areas. However, these parameters were also susceptible to variations due to plant age and might also have been affected by the environment.

Low dry matter production in the cultivar types B and C (Table 2) might be partially explained by their pattern of shoot and leaf development.

In Around the World and Pie Pip low biological yields were probably the result of excessive leaf production and retention (average of 13 % above the mean leaf number over all cultivars), particularly during early growth during the dry season. Large reductions in crop growth rate at high leaf area indices were recorded in cassava (CIAT 1973) presumably due to excessive mutual shading and little vertical separation between leaves. With the short petioles and internodes in these two cultivars, the lower shaded leaves may be below compensation point which would hasten leaf fall.

The small individual leaf sizes and short leaf area duration would also lead to lower yield potential in Around the World and Pie Pip respectively.

The low dry matter production per plant of Maracas Blackstick compared with other cultivars might be explained by the low leaf number present throughout growth (39 % less than mean leaf number over all cultivars), resulting from the lack of branching. However, individual leaf growth and duration characteristics were suitable for high dry matter production in this cultivar which had the largest leaves, good leaf display and long leaf area durations. In fact, Maracas Blackstick had the highest dry matter production per leaf retained after 46 weeks of growth (6.52 g (nm) $leaf^{-1}$), when compared with the highest (Redstick 5.5. g (nm) $leaf^{-1}$) and the lowest (Pie Pip 2.84 g (nm) $leaf^{-1}$) yielding cultivars. The harvest indices of the three cultivar types (Table 2) could also be explained on the basis of their vegetative development.

Earlier, it was suggested that there might be a physiological barrier between high dry matter production and high harvest indices (Wholey & Cock, 1974, and Holmes & Wilson, 1976). With the need for a high number of meristems per plant to maintain the leaf numbers necessary for maximum biological yield, there will always be a strong shoot sink in existing high dry matter cultivar types. This sink will include meristems in the stem apices and young developing leaves receiving assimilate from mature leaves in the upper part of the canopy (Thrower, 1962). Thus the shoot presents as a highly competitive sink, particularly during tuber bulking which is coincident with the period of rapid branching in the cultivars studied.

On the basis of the work in this and our earlier paper, it is possible to suggest that the ideal high yielding cassava types will be those in which the apparent barrier between high biological yields and high harvest indices is broken. this coulb be achieved in a type with rapid early branching to give optimum numbers of well displayed large leaves, and in which further maintenance of the assimilatory surface during ontogeny is by long leaf duration rather than continued high rates of leaf production.

The identification of an annual cassava cultivar in which shoot senescence occurs at tuber maturity would further enhance distribution of assimilate into the tubers.

Cultivars with these characteristics have been tentatively identified here and in other collections and the subsequent synthesis of these characteristics into a single pure breeding line would be the objective of a hybridization programme.

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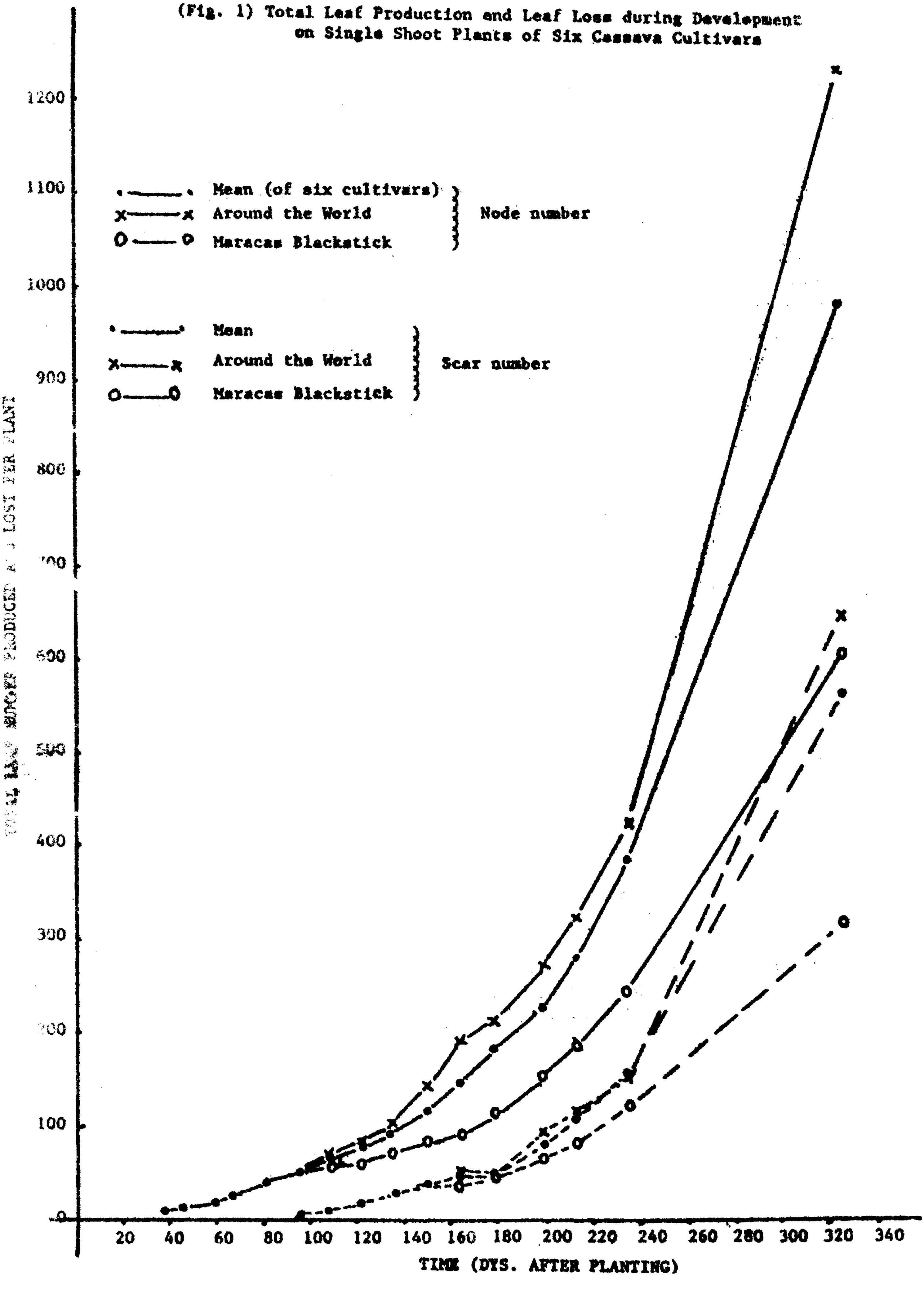
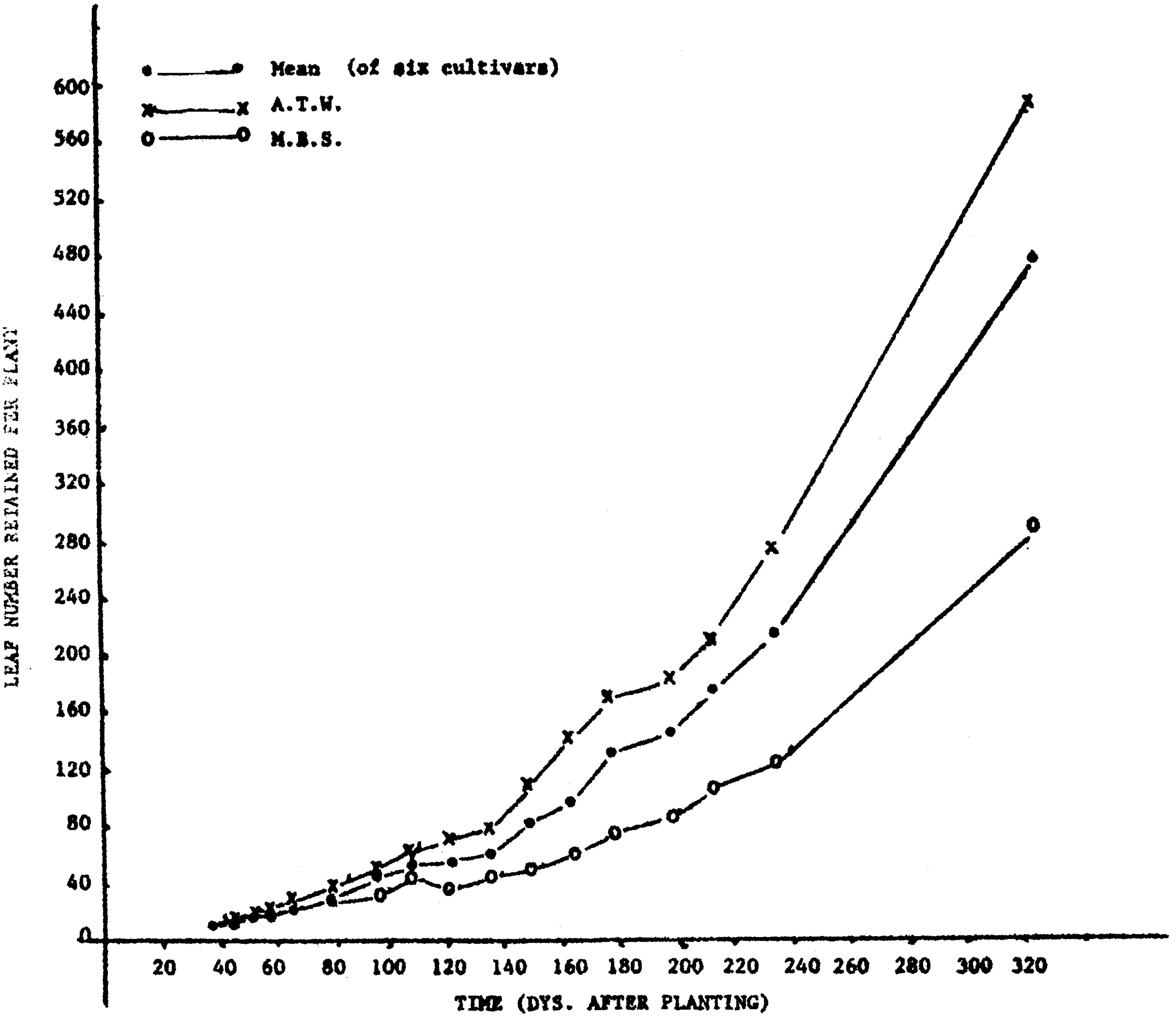
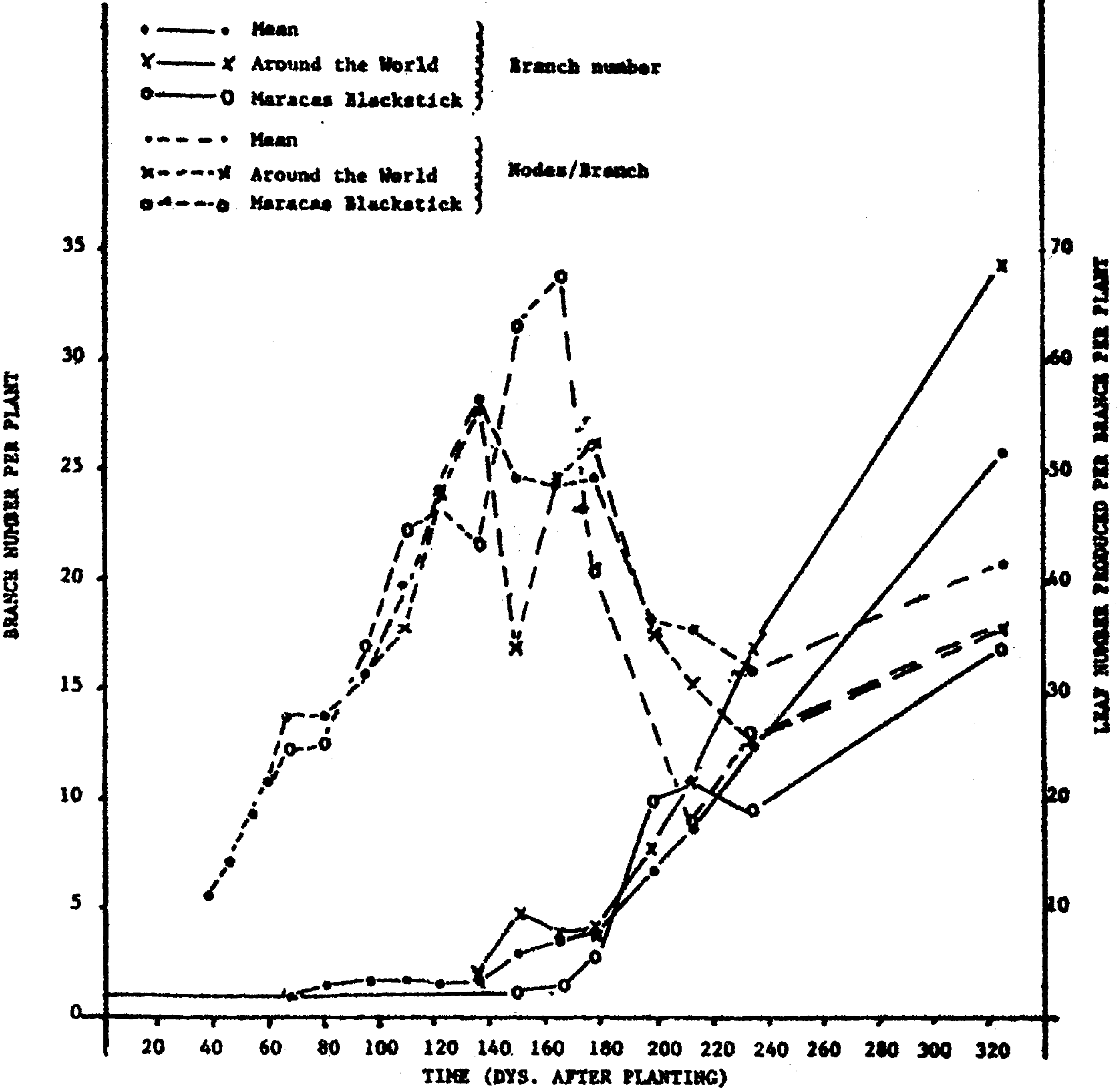
(Fig. 1) Total Leaf Production and Leaf Loss during Development on Single Shoot Plants of Six Cassava Cultivars



(Fig. 2) The Number of Leaves Retained during Ontogeny In Single Shoot Plants of Six Cassava Cultivars



(Fig. 3) Branch Production and Rates of Node Production per Branch in Single Shoot Plants of Six Cassava Cultivars



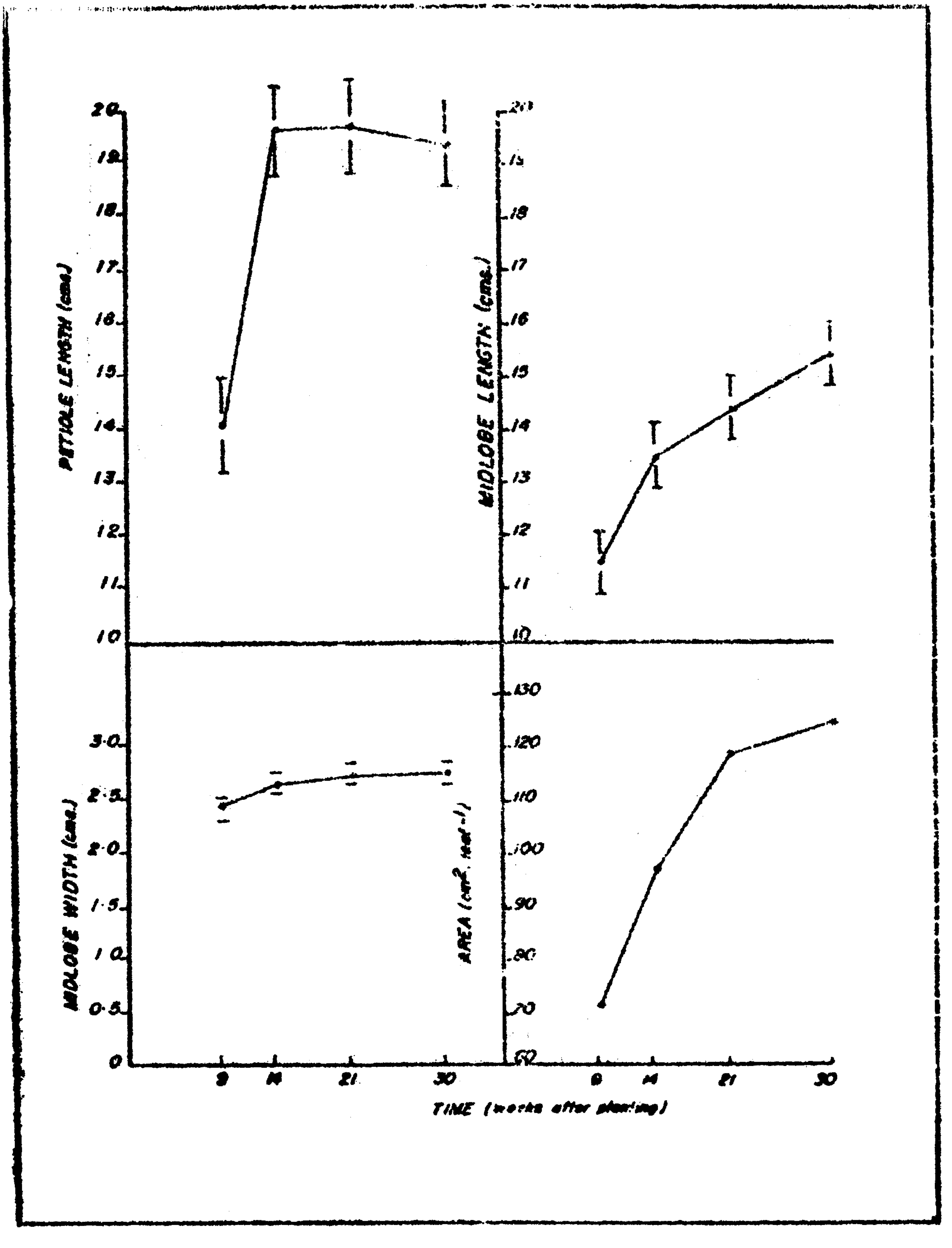


Fig. 4 - The Effect of Plant Age at the time of leaf appearance on the mean leaf quantitative morphology of six cassava cultivars.

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ABSTRACT

A study was made of the quantitative shoot morphology, development of individual leaves and their relationship to biological and economic yield in six Trinidad Cassava *(Manihot esculenta* Crantz) cultivars. Two cultivar types were identified on the basis of leaf production and retention characteristics. These cultivar differences were related to the number of apical meristems produced and only became evident after the onset of branch production. There were no cultivar differences either in the pattern of leaf production per branch or in percentage leaf loss, during development, but there was evidence of genetic differences in the pattern of leaf development, particularly leaf size and leaf duration. These parameters showed variations which could be ascribed either to plant ontogeny or the prevailing environmental conditions. Reasons for low dry matter production and low harvest indices in the six cultivars are discussed in relation to differences in shoot and leaf development outlined.