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SOME PHYSIOLOGICAL ASPECTS OF YIELD IN CASSAVA (*MANIHOT ESCULENTA* Crantz)

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SUMMARY

The importance of dry matter production and factors affecting it, such as leaf area index and leaf inclination, are discussed. The relative importance of dry matter production and its distribution in relation particularly to spacing are reviewed.

The author suggests a plant ideotype based on these observations.

RESUME

L'importance de la production de la matière sèche et les facteurs qui l'affectent, tels que l'index de la zone foliaire et l'inclinaison des feuilles ont été abordés. L'importance relative de la production de la matière sèche et de sa distribution surtout par rapport à l'espacement ont été passés en revue.

L'auteur propose un idéotype végétal fondé sur ces observations.

RESUMEN

Se discute la importancia de la producción de materia seca y los factores que la afectan, tales como el índice de área foliar y la inclinación de la hoja. Se revisa la importancia relativa de la producción de materia seca ya su distribución en relación, particularmente, con el espaciamiento.

El autor sugiere una planta ideotipo basado en esas observaciones.

INTRODUCTION

The physiology of *Manihot esculenta* Crantz has received little study. In this paper I shall endeavour to assess some of the physiological variation present within the species that may be used to produce higher yielding types.

For high productivity of carbohydrate it is necessary to have (a) high dry matter production and (b) favourable distribution of dry matter to the economically useful root tubers. Harvest index, the economic yield divided by total yield, can be used to describe this distribution.

MATERIALS AND METHODS

a) CMC 84, a high yielding cultivar, was grown at 1 x 1m spacing, and observations on its growth were taken at seven intervals, up to sixteen months after planting.

b) Cultivars CMC 84, CMC 39 and Llanera were planted at plant populations ranging from 3,000 to 30,000 plants/ha using a systematic design of the type described by Bleasdale². Harvests for fresh yield, dry yield and total dry matter were taken at three, five, seven and eleven months. All results use a three point moving average.

c) Four cultivars, M Colombia 22, CMC 39, M Colombia 1080 and M Mexico 12, were also planted in the systematic spacing design.

Leaf area index was estimated using the grid method and interception of total radiation was measured using Monteith type solarimeters four to five months after planting. Leaf angle was estimated by measuring the angle between the midrib of the central lobe and the horizontal.

d) Eighteen cultivars of different gross morphology were compared in an unreplicated trial; Llanera was repeated three times as a check, making a total of 20 plots. Plant population was 20,000/ha and harvests were taken at approximately 120, 180, 240, and 360 days. Data were corrected to the exact date.

The other trials referred to are described in the text.

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DRY MATTER PRODUCTION

Dry matter production depends on the absorption of light and its utilization by leaves to produce carbohydrates from CO_2 and water. It is obvious that to obtain high levels of production it is necessary to absorb as much of the incident radiation of effective wavelengths as possible, then to use it efficiently in photosynthesis.

To intercept as much incoming light as possible it is necessary to have a sufficient leaf area index. Cultivar CMC 84 was grown for almost a year and a half on a soil of good water-holding capacity without prolonged water stress. The leaf area index was never greater than 2.2 and was less than 1.5 for most of the growth period (Fig. 1). This is considerably less than leaf area indices quoted for some other crops (e.g. cotton, 3 to 7.6⁸; kale, 3.5 to 5^{14,15}) which do not have erect leaves.

In another experiment, the leaf area index of CMC 84 was modified by leaf clipping and apex removal, the crop growth rate (corrected for the apices removed and clipped leaves) had not apparently reached a plateau level at LAI of 3 to 4 (Fig. 2). Sinha and Nair¹² and Doku⁴ have reported differences in leaf area duration between cultivars and related these to yielding ability.

In a study of LAI development in eighteen cultivars, Colombia 113 retained its leaves during its total growth period whereas, with most cultivars there was a marked decline in leaf area index after 180 days (Fig. 3). This decline was particularly pronounced in cultivar Colombia 22.

A series of experiments were performed to investigate the causes of leaf fall. Leaves covered with silver paper abscised and fell within a few days, whereas uncovered leaves remained attached for a longer period. This suggests that light on the surface of the lamina is one factor necessary to prevent leaf fall (Table 1). Leaf fall was not, however, solely the result of shading since all leaves fell sooner or later, even if normally exposed to light. When the plant apices were removed, leaf fall was delayed, suggesting a direct influence of the apex itself (Table 1).

Leaf fall causes a substantial loss of dry weight from the plant. In cultivar CMC 84 it was estimated as more than two t/ha during the period from three to five months after planting. When apices were continuously clipped to prevent the formation of new leaves, leaf fall was reduced to 1.3t/ha (Table 2). No reduction in crop growth rate was observed as a result of this treatment, showing that the remaining old leaves can continue photosynthesis efficiently (Fig. 2). This suggests that plants could produce and retain more dry matter if they produced fewer leaves, but retained them for a longer time and hence giving a larger leaf area index because of reduced leaf loss.

The dry matter production of Colombia 113 was similar to the mean of the other cultivars up to 120 days, as was its leaf area index, suggesting a somewhat similar efficiency of assimilation (Figs. 3,4). After 120 days the greater production of dry matter in Colombia 113 can be ascribed to its increased leaf area index. Colombia 22, on the other hand, always has a small leaf area index in comparison with the mean, and yet its total dry matter accumulation was remarkably similar. To speculate on these somewhat limited data, it would appear that there may be differences in the efficiency of photosynthesis either of the canopy or of the individual leaf that can be used to give higher yielding potential. Unfortunately, I know of no direct measurements made of photosynthesis on this crop. These are desperately needed to increase our understanding of its productivity in terms of dry matter.

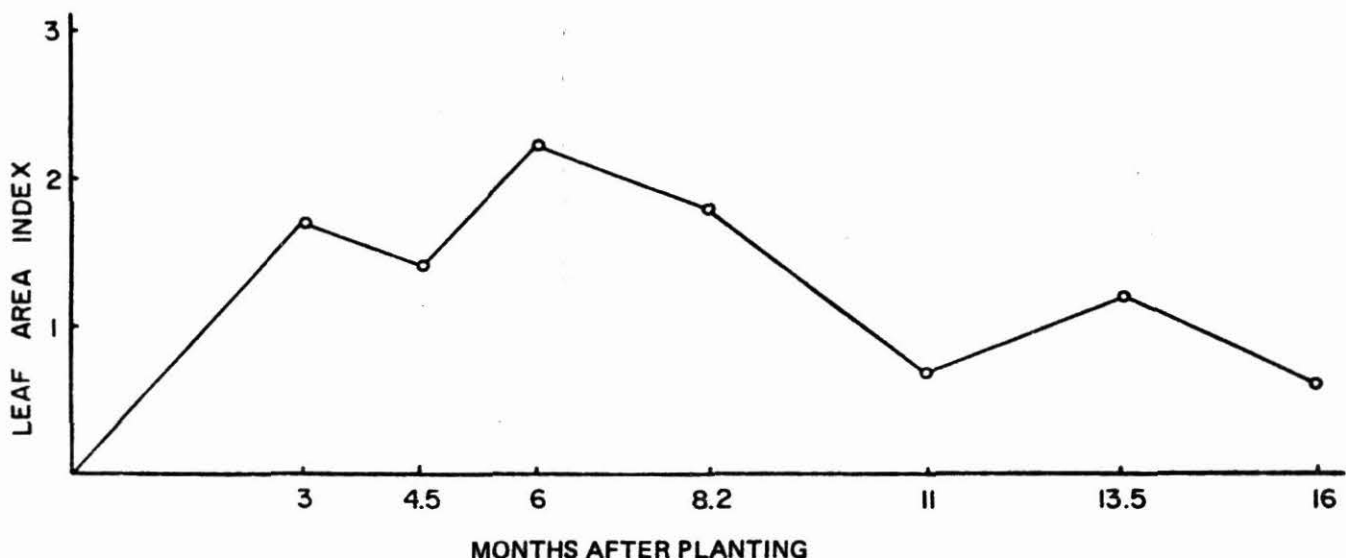


Figure 1: Changes in leaf area index of CMC 84 with time

Photosynthesis is not a linear function of light intensity above a certain level. Consequently, it is not sufficient just to have a crop canopy that intercepts all the incoming radiation. It is necessary to intercept almost all the light in such a manner that a large proportion of the leaves receive a low level of illumination that is still nevertheless sufficient to support photosynthesis.

In the tropics where the sun angle is high, this can be achieved by having more erect leaves. This is especially important in the middle of the day when the light intensity is greatest. At this time the elevation of the sun is nearly vertical and will illuminate leaves at low intensity when they tend to be more vertical. Williams¹⁶ also showed that leaf conductivity fell, showing a reduction in stomatal aperture, during the day after reaching a maximum in the morning. This suggests the possibility that leaf angle changes were asso-

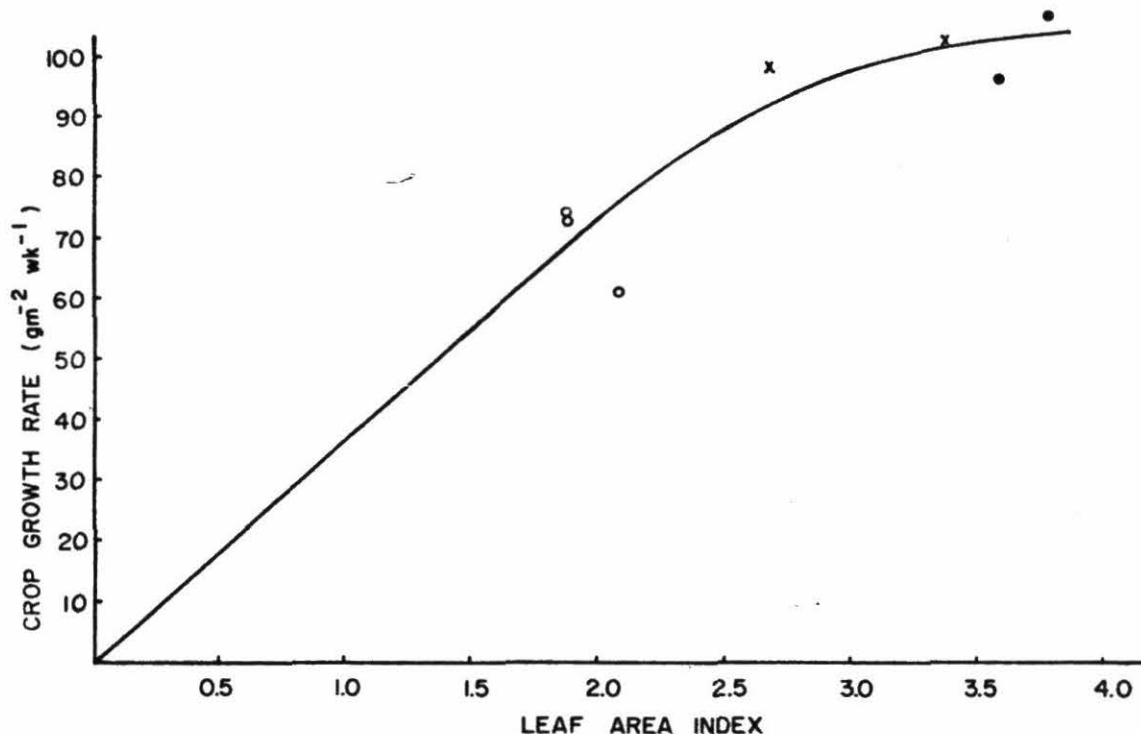


Fig.2: Crop growth rate of CMC 84 from 3 - 5 months as related to leaf area index. The leaf area index was modified by cutting the apex (x) by leaf clipping (°) and control (°). (Source: Cock and Acuña unpublished).

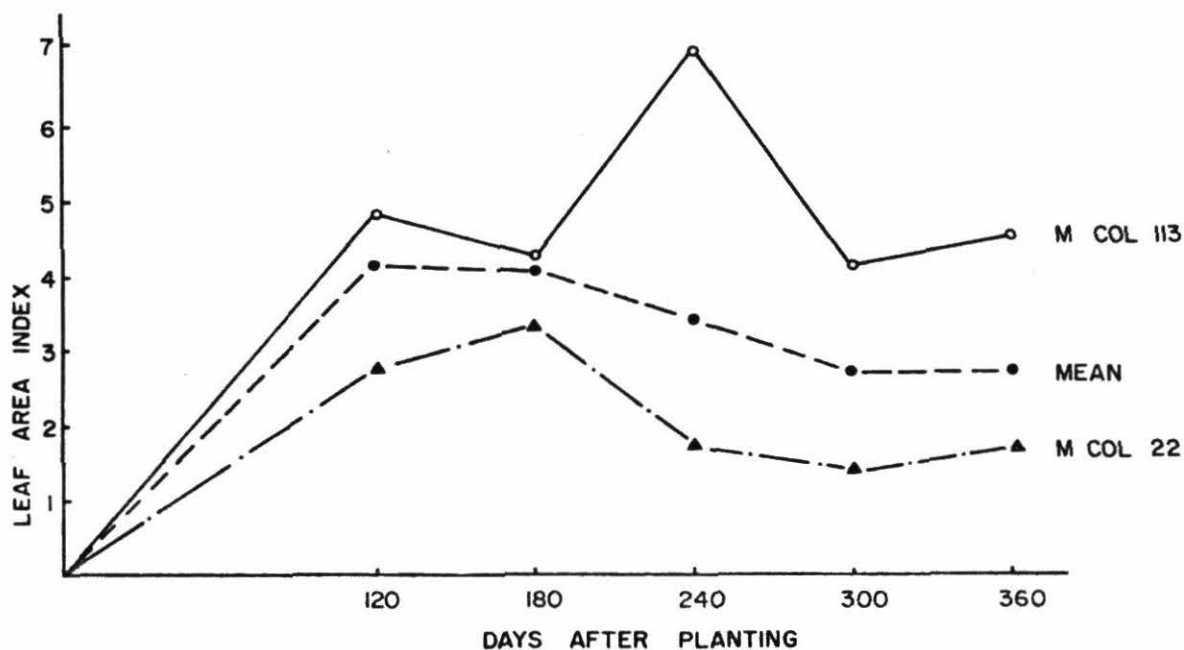


Fig.3: Leaf area index of M Colombia 113 and 22 compared with the mean of sixteen varieties.

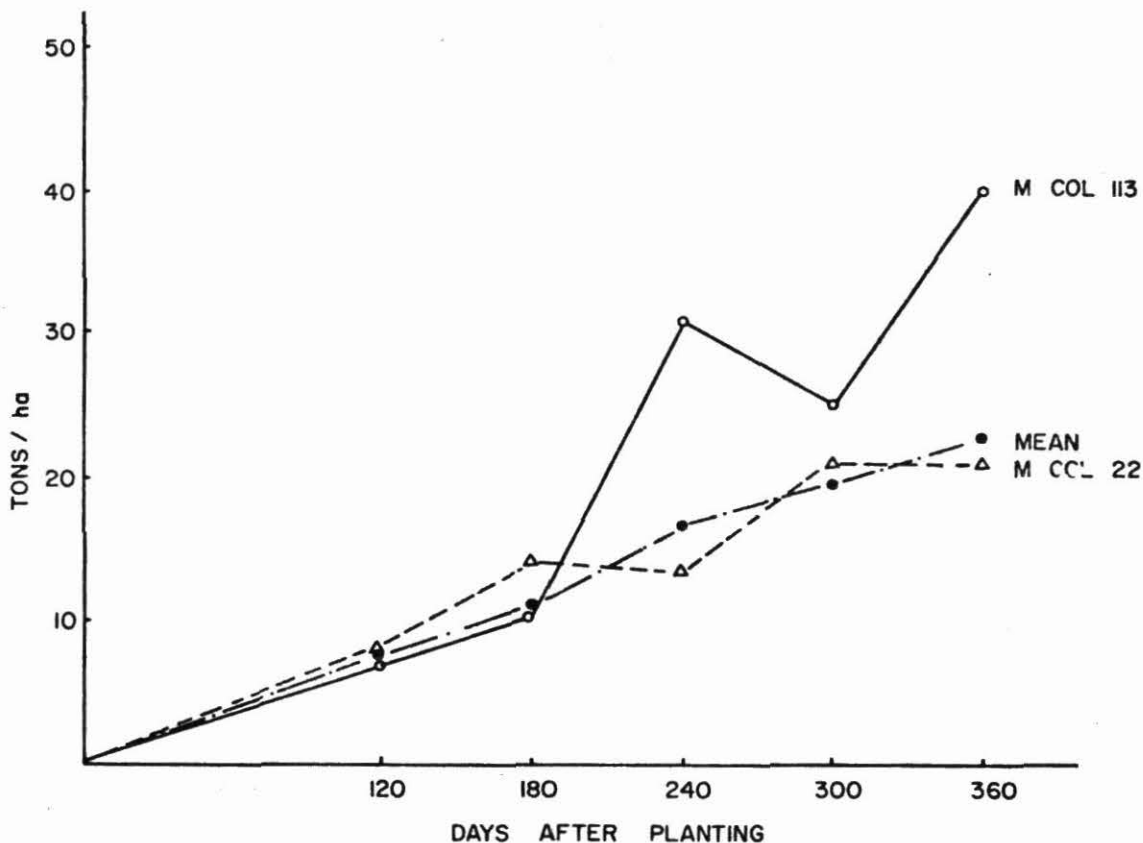


Fig 4. Changes in total dry matter of M Colombia 113 and 22 and the mean of 16 other varieties.

ciated with wilting and stomatal closure. It can be seen that this may not be the case, in cultivar Ecuador 44 the stomatal resistance of an upper leaf apparently decreased as the leaf became more vertical (Fig. 5). The lower leaves show less leaf angle change which could be advantageous. When leaf area index is small, it is necessary to have the lower leaves horizontal so as to absorb all the light which penetrates to the lower levels of the canopy.

The interception of total radiation was measured in four cultivars of cassava at midday on a clear day. There were large differences in the extinction co-efficient (Fig. 6). The extinction coefficient is closely related to the leaf angle (Fig. 7). Consequently it appears that there is a large degree of variability in leaf angle that can be used to obtain uniform light interception within the crop canopy, and that this is not associated with the detrimental effects of midday stomatal closure.

HARVEST INDEX

The potential production of root crops has been suggested as substantially greater than that of the grain crops. One of the reasons is that a crop such as cassava that may grow for twelve months, starts filling its storage organs after about two months (Wholey and Cock, unpublished) and hence uses more than 80% of its total growth period in what may be described as the productive phase. A cereal crop such as rice that grows to 120 days has thirty days of productive phase, representing only 25% of its total growth period. Improved rice cultivars have harvest indices of about 50%, and one might expect high values in cassava.

In the trial with eighteen cultivars, harvest indices reached only a mean value of 36%. The two highest yielding cultivars Colombia 113 and 22, however, had indices of 54% and 57% respectively, and there was a reasonably close correlation between yield and harvest index. Selection for this character could lead to higher yielding types (Fig. 8). The low mean value of harvest index may possibly be ascribed to the dense plant population (about 20,000 plants/ha).

After seven months growth the harvest index of three cultivars showed a sharp decline as a function of increasing plant population (Fig. 9) and also a decline in dry matter root (tuber) yield with increasing plant population (Fig. 10) above an optimum density which however was different for each cultivar. By eleven months the decline in harvest index was less pronounced in CMC 39 and only occurred at high plant populations in CMC 84.

The data from Llanera were variable and difficult to interpret (Fig. 10). However, there was no evidence of the steep decline seen at seven months (Fig. 9). It appears that not only are there differences in harvest index but also that some cultivars can withstand more dense plantings than the others without adverse effect on their harvest index.

Increased production of crops has to a large extent been associated with the increased use of fertilizers, particularly nitrogen. Consequently, reports that high levels of nitrogen may increase foliage production at the expense of roots are disconcerting.^{5,7} This is in spite of reports suggesting a neutral or positive yield response to nitrogen^{1,3,6,7,11}. In a trial in which up to 300 kg N were applied there was an indication of increased yield with increasing levels of N, but this trend did not reach statistical significance. There was no significant difference between the weight of the aerial parts of the plant at the different nitrogen levels (Fig. 12). Consequently, cultivars such as Llanera may be able to utilize increased nitrogen levels without decreasing harvest index.

GENERAL

Productivity does not depend on just one of the two components discussed in the previous two sections. It depends on the successful combination of the two.

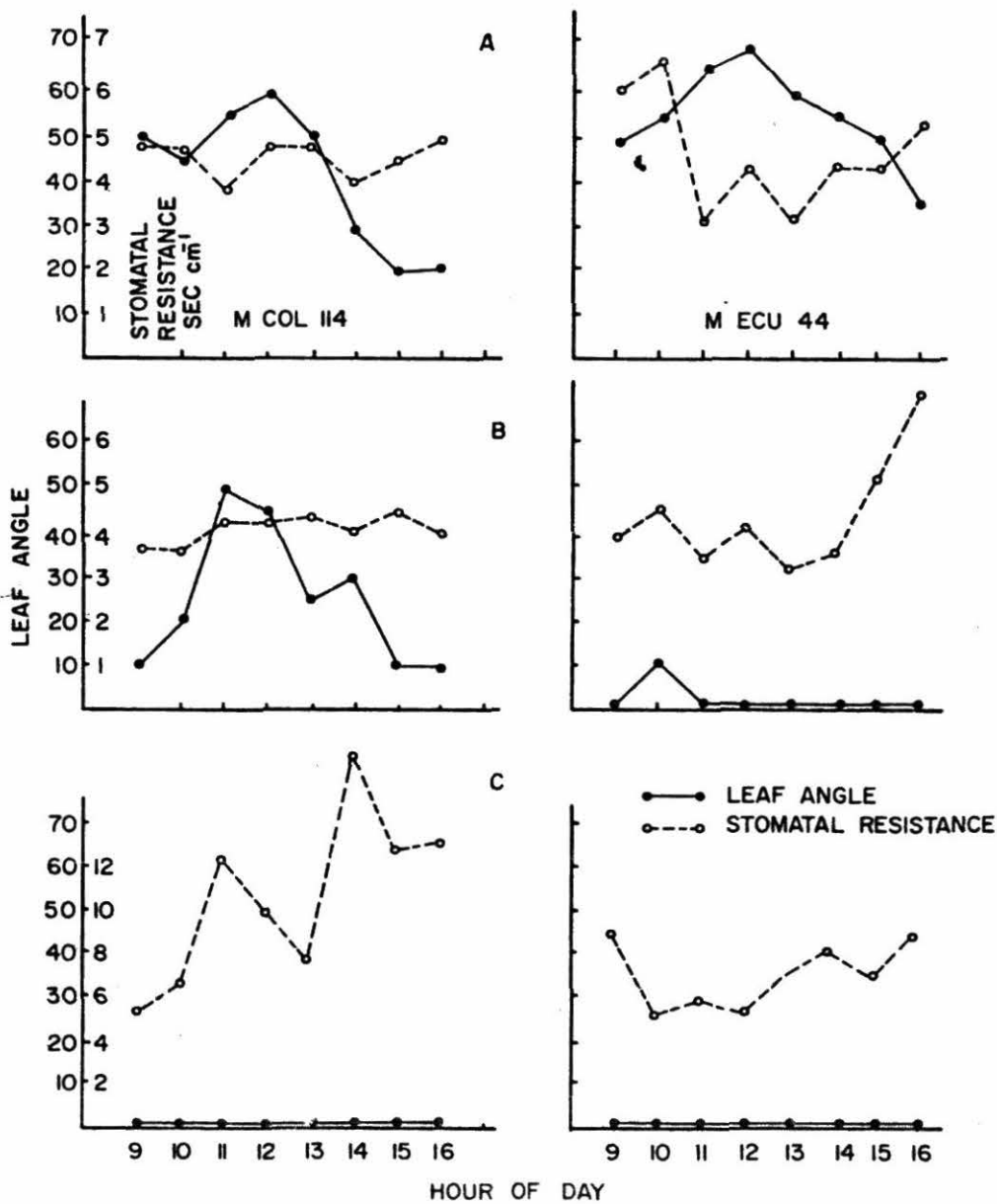


Fig.5: Leaf angle changes in two cassava varieties.
A. Upper leaf, B. Middle leaf, C. Lower leaf

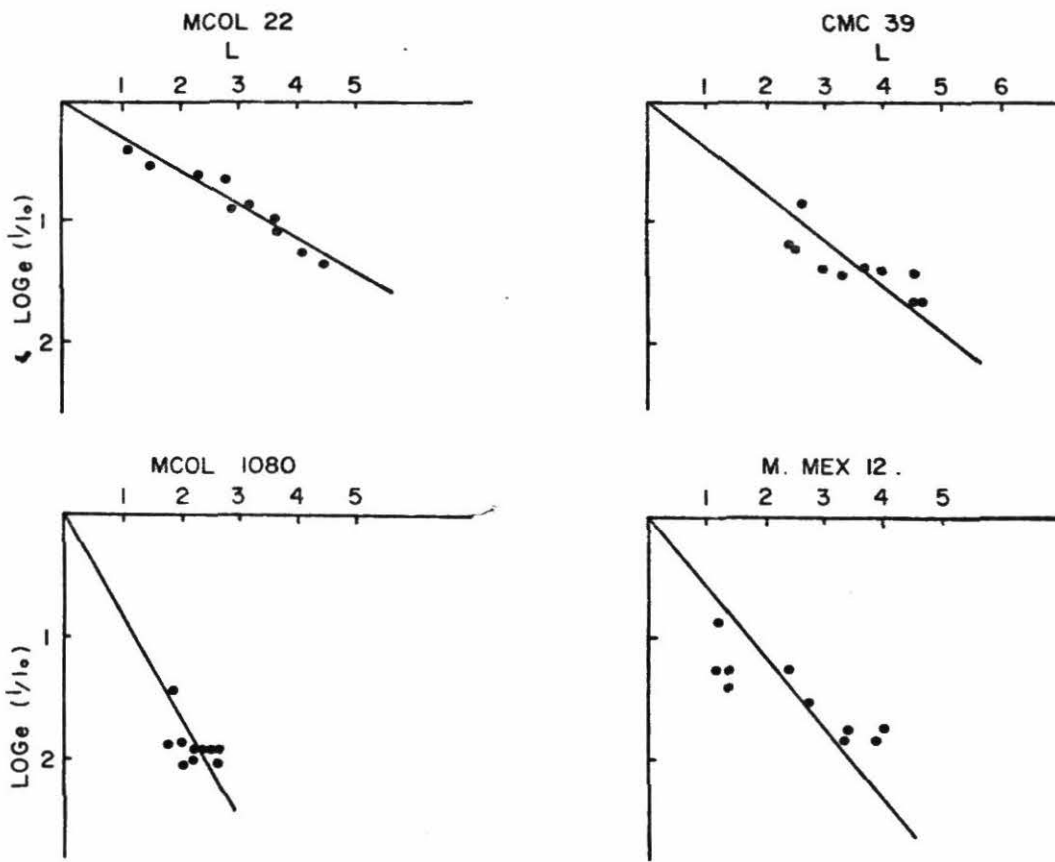


Fig.6: The relation between light interception and leaf area index (L) four varieties of cassava (I_0 is radiation above crop, I is radiation below crop).

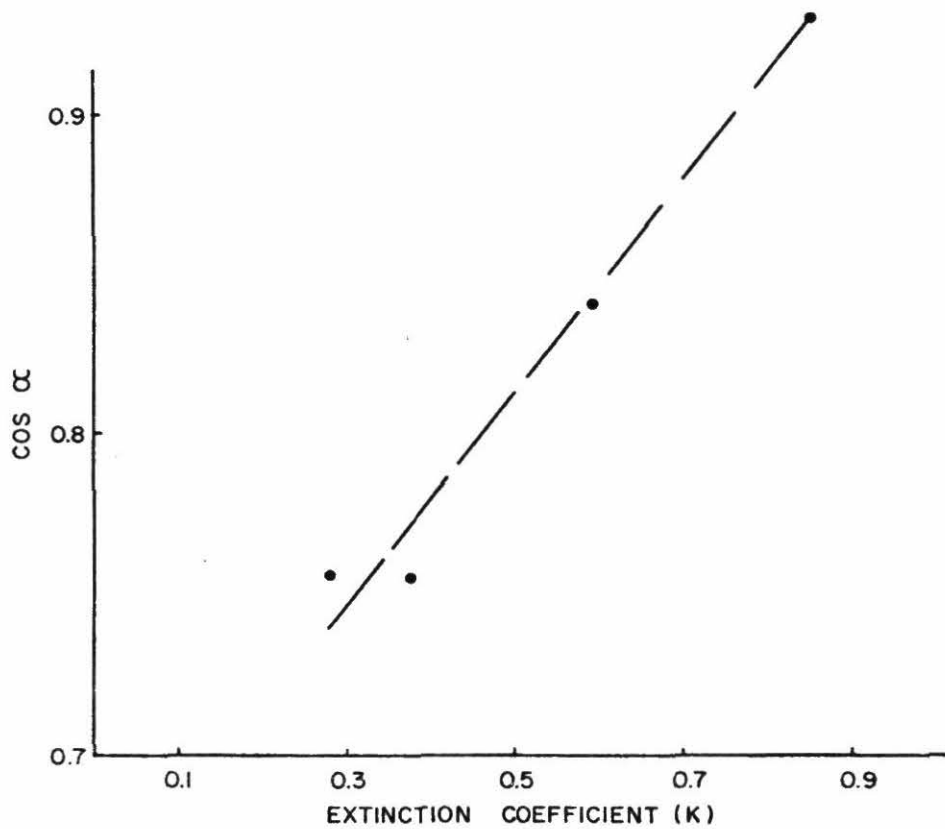


Fig.7: The relation of the light extinction coefficient (K) to the cosine of the leaf angle ($\cos \alpha$)

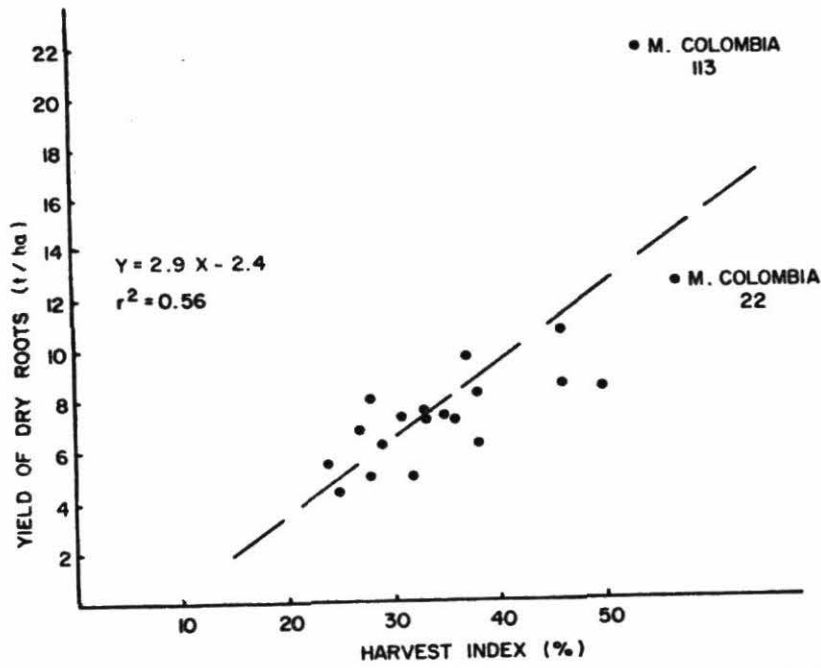


Fig.8: Relation ship between yield of dry roots and harvest index 360 days after planting .

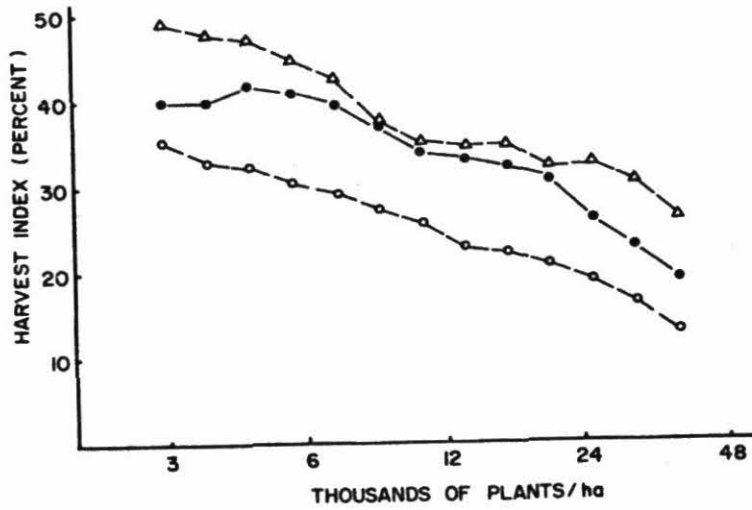


Fig.9. Harvest index of CMC 84 (●-●), Lianera (▲-▲) and CMC 39 (○-○) at 7 months (i) and 11 months

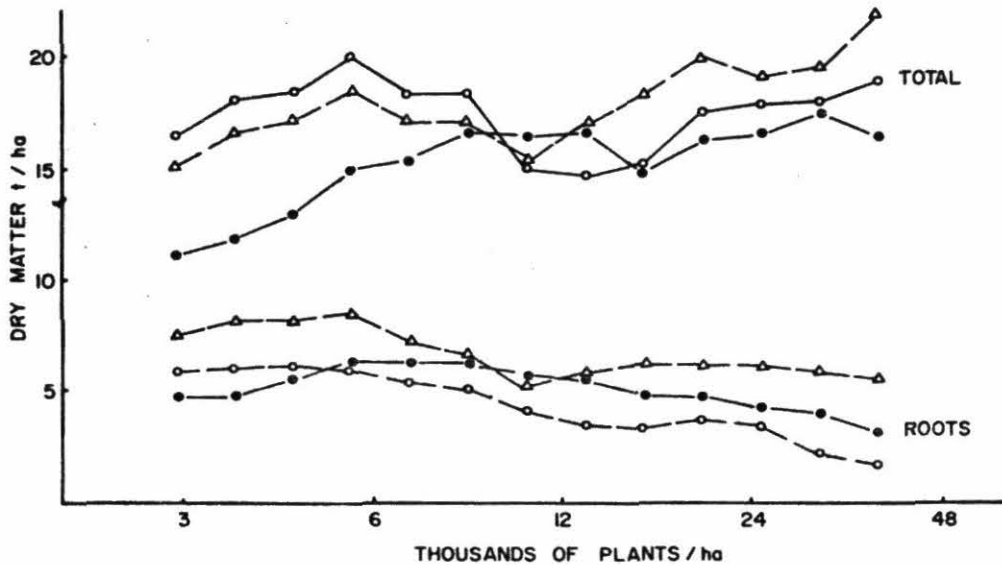


Fig.10: Changes in total and root dry weight of Lianera (▲-▲), CMC 84 (●-●) and 39 (○-○) at different plant populations after 7 months .

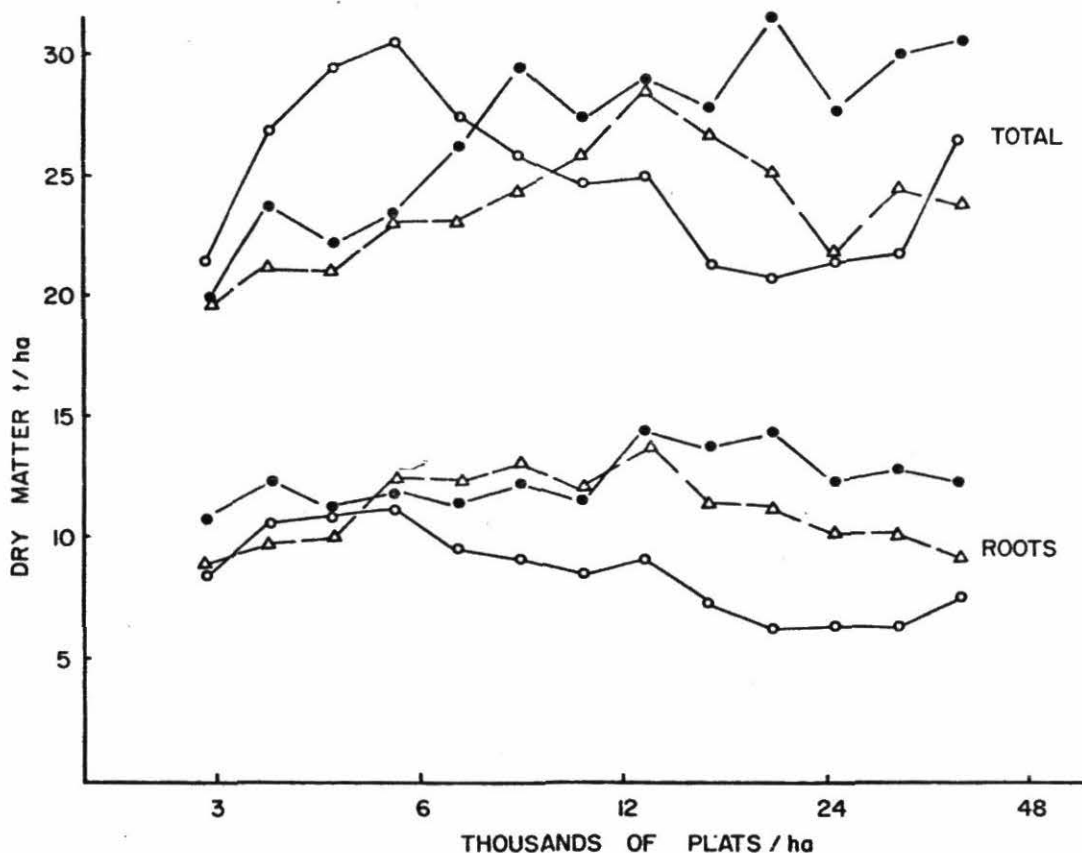


Fig. II: Changes in total and root dry weight of Lianera (Δ - Δ), CMC 84 (\bullet - \bullet) and CMC 39 (\circ - \circ) at different plant populations after 11 months.

In general cassava does not have sufficient leaf area for maximum dry matter production after six months. One way to increase leaf area is to increase plant population, but this leads to a crop in harvest index in certain cultivars. It appears that cultivars can be found that can withstand high plant populations.

CMC 84 increases its dry matter production with increasing plant population and harvest index only declines at the higher populations used. Thus its total dry root yield tends to increase with increasing plant population up to about 20,000 plants/ha (Fig. 11). In contrast, tall variety CMC 39, lodged at high plant populations and showed a decline both in total dry matter production and in harvest index at high plant populations. (Figs. 10, 11).

CONCLUSIONS

From the results presented, the cassava breeder seeking high yield potential should try to combine first of all:

1. A short stature that will give a low dry weight of stem and hence a potentially high harvest index.
2. Retention of leaves so as to maintain a large leaf area index.

As the level of breeding becomes more refined, he may also search for (a) low rate of leaf and inter-node production to produce a minimum of stem dry matter, (b) erect leaves during the middle of the day to use light efficiently in photosynthesis and to illuminate the lower leaves to delay leaf fall, (c) the ability to maintain a large harvest index at high nitrogen levels and plant population which give a rapid build up of leaf area index even in varieties with low rates of leaf production.

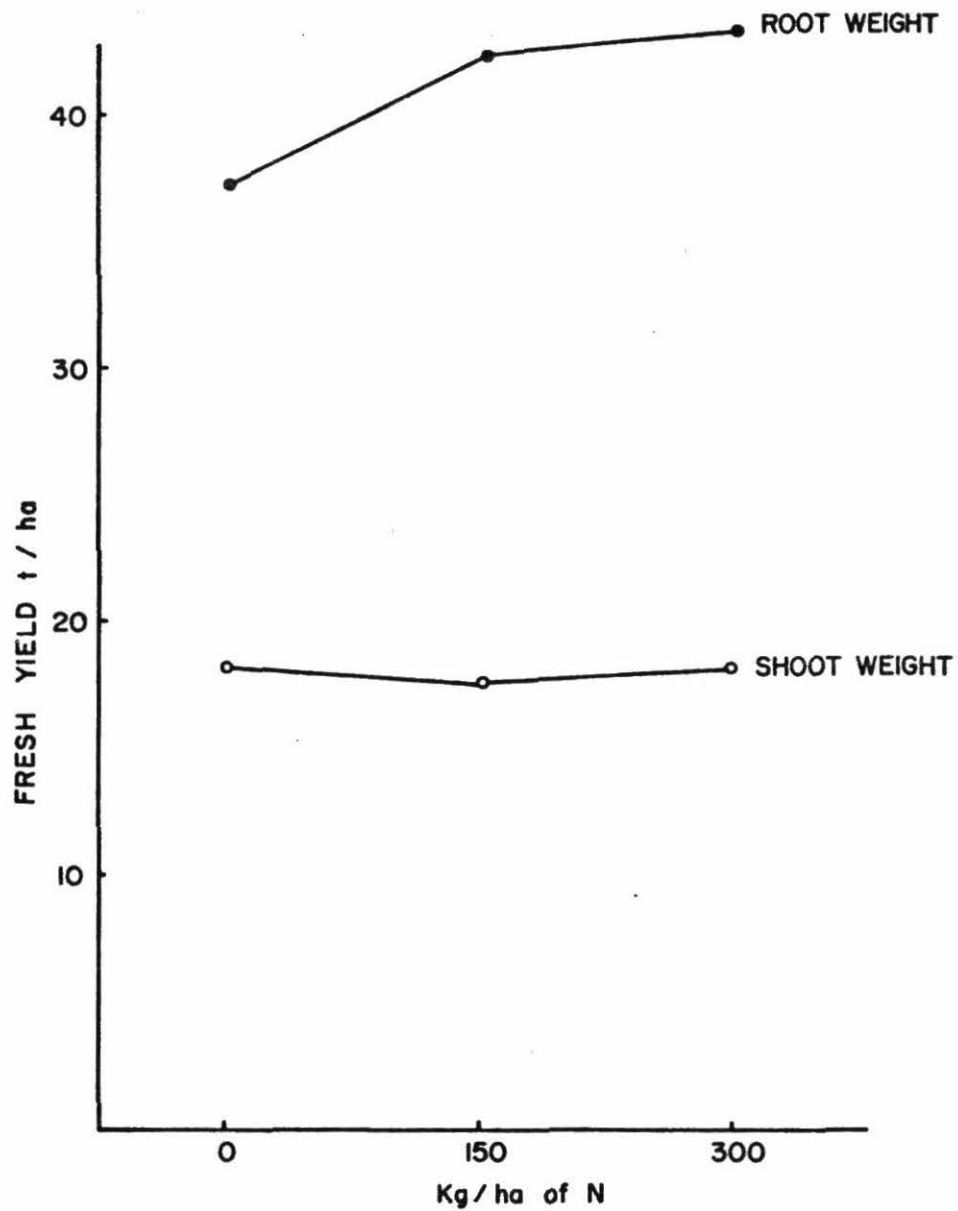


Fig.12. Response to nitrogen of Llanera. The nitrogen at 150kg/ha was applied all at planting, all at 3 months or half at each time. The nitrogen at 300kg/ha was applied all at planting or 3 months or split at planting and 3 months, 3 months and 6 months or planting, 3 months and 6 months. The means are presented here. Growth duration: one year .

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TABLE 1

Effect of various treatments on time of leaf fall (days to the time when the third of five marked leaves fall).

Treatment	With Apex	Apex Removed
All leaves removed except five	26	61
Five leaves covered with silver paper	8	9
Leaf lamina of five leaves removed	7	7
Part of leaf lamina of five leaves removed	19	20
Control	42	61

L.S.D. = 12.4 (p = 0.05)

TABLE 2

Leaf fall data of CMC 84 from 3 to 5 months after planting (Source: Cock and Acuna, unpublished)

	Leaf fall t/ha	Leaf fall leaves/plant/week
Control	2.1	17.8
Apex removed	1.3	7.6