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Response of cassava to water stress

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Key words Leaf area index *Manihot esculenta* Root characteristics Water stress Yield

Summary Cassava (*Manihot esculenta* Crantz) is a staple food for a large sector of human population in the tropics. It is widely produced for its starchy roots by small farmers over a range of environments on poor infertile soils with virtually no inputs. It is highly productive under favorable conditions and produces reasonably well under adverse conditions where other crops fail. The crop, once established, can survive for several months without rain. There is a wide variation within the cassava germplasm for tolerance to prolonged drought and the possibility to breed and select for stable and relative high yields under favorable and adverse conditions does indeed exist. Research with several cassava clones at CIAT has shown that high root yield under mid – term stress is not incompatible with high yield under nonstress conditions. Plant types with high yield potential under both conditions (*e.g.* the hybrid CM 507-37) are characterized by having slightly higher than optimum leaf area index under nonstress conditions, higher leaf area ratio and more intensive and extensive fine root system.

I. Introduction

Cassava (*Manihot esculenta* Crantz) is a major staple crop ;and one of the primary sources of food energy in the diet of several hundred million people in the tropics[4,5]. Its starchy roots are the harvestable product, consumed either fresh or after processing. The leaves are edible, once cooked, and are commonly eaten in several tropical countries[11]. In addition to its use as a human food (approximately 60–70% of total production) in Africa, South America and Asia, cassava is also used for animal feed, starch and alcohol production.

The cassava plant is a perennial shrub, of the Euphorbiaceae, known only in the cultivated form and originally domesticated in South and Central America. After the conquest of the Americas, cassava spread to Africa and Asia, where its current production exceeds that in its center of origin. It is grown over a wide range of environments (between 30°N and S latitude) and at elevations that range from sea level up to 2000 m near the equator. Nevertheless, most cassava is grown in areas where the annual mean temperature is above 20°C and the rainfall is more than 700 mm per year[5,10].

Cassava is often grown in monoculture; however, mixed cropping is the most common production system with tree crops, annual legume and cereal crops[9,12,14]. Cassava is mainly cultivated by small farmers on small plots of poor, infertile acid soils, usually without application of fertilizers and pesticides[8]. In most areas of cassava production, the crop has to

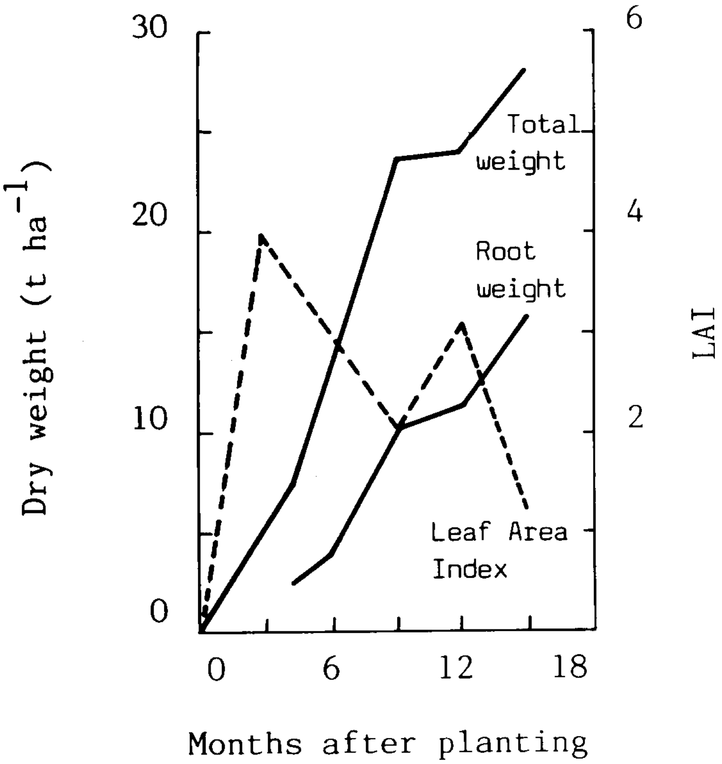

Fig. 1. Growth and development of a typical cassava crop. (Source: Cock, 1985).

endure a prolonged dry period of several months without rain. Under these stressful conditions, cassava can produce from 3 to 5 t ha^{-1} dry roots annually, whereas most other annual food crops would fail. This ability to produce under adverse edaphic and atmospheric conditions has earned cassava the reputation of being a "famine reserve crop"[5].

II. Growth and development

Commercial planting of cassava is from woody stem cuttings (15 to 20 cm long), planted directly after the harvest of mature plants or after several months' storage of long stems under shade. The cuttings may be planted horizontally, vertically or inclined in flat land, ridges or in mounds of soil at a population density of 7000 to 20000 cuttings ha^{-1}. Most cassava planting takes place at the onset of the rainy season; but in some cases, cassava farmers plant towards the end of the rainy season. After planting, one or more of the auxillary buds on the top of the cutting sprout into shoots. Roots initiate mainly from recently formed callus tissues from the base (basal roots) and the lower nodes (nodal

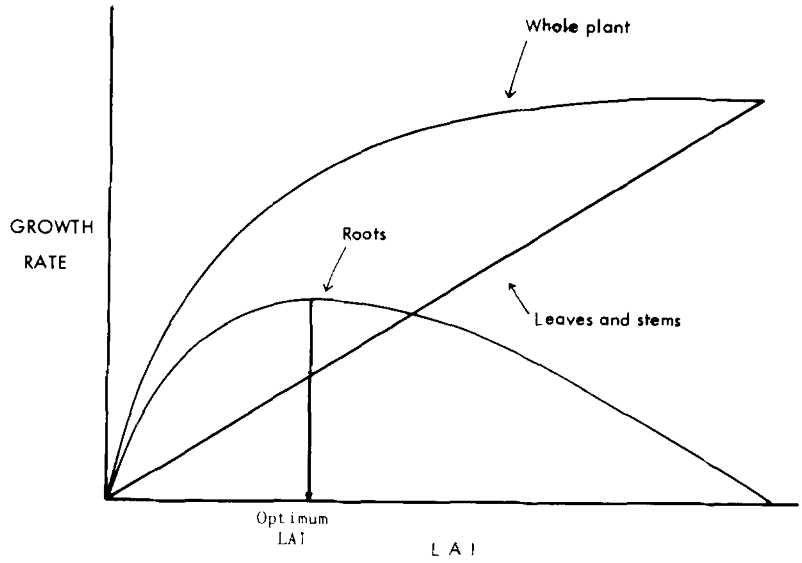

Fig. 2. Schematic representation showing relation between whole plant growth, partitioning of growth between stem (and leaves) or roots, and the leaf area index (LAI). The *vertical arrow* indicates optimum LAI for root growth. (Source: Cock, 1984).

roots) of the cutting[16]. During the first few weeks of crop establishment, the plants form a fibrous root system, mainly in the upper layer (1 m) of soil[7]. About 2 to 3 months after planting, some of the fibrous roots (from 5–15 roots per plant) start to expand rapidly, forming storage roots for starch. These storage roots continue to accumulate starch and to increase in weight during the growing season until the crop is harvested, 8 to 15 months after planting (See Figure 1). However, when the crop is kept for a longer period before harvest, as practiced often by cassava farmers, the quality of fresh roots for human consumption deteriorates and the crop is mainly processed for food products, animal feed and starch extraction.

The formation of leaves in cassava has preference for available assimilates over storage roots in the first 3 months of growth. However, after this period, cassava continues to form new leaves concurrently with storage root filling. The leaf area index (LAI) — leaf area per ground unit area — increases in the first 3 to 6 months and then declines gradually as the older leaves in the lower strata of the canopy fall. The maximum LAI in cassava ranges from 4 to 8, depending upon the cultivar and the atmospheric and edaphic conditions prevailing during crop growth[4].

The continuous development of the source (leaves) and the sink (roots) for carbohydrates in cassava is in contrast with that of cereal crops. In cereal crops such as maize, sorghum, millet, wheat and rice, there are two stages of crop development; namely, vegetative and reproductive. During the vegetative stage (about 70 to 75% of the growth cycle), the leaves, stems and inflorescences develop, followed by a shorter reproductive stage (25 to 30% of the growth cycle), during which grain filling with carbohydrate occurs. With this pattern of crop development and growth in cereals, no competition exists for partitioning the photosynthetic assimilate between source and sink development. In cassava, however, the current photosynthetic assimilates are partitioned between the leaves and the roots, leading to competition between the two organs. This pattern of growth results in an optimum LAI for storage root production (See Figure 2). The balance between formation of leaves and filling of roots is controlled by both genetic and environmental factors.

III. Effect of soil water stress

The response of cassava to water stress was studied using a drainage field lysimeter 30 m × 15 m × 2.3 m deep that was constructed in 1981 at the Santander de Quilichao experiment station of CIAT, Colombia[2]. The bottom of the lysimeter was covered with 0.3 cm layer of black asphalt and drainage tubes were installed 3 m apart and covered with a 10 cm layer of sand and gravel. The tubes drained excess water, due to rainfall or irrigation, to a nearby 5 m × 3 m × 1 m reservoir. The whole area of the lysimeter is protected from lateral water flow by a brick wall extending to within 1.3 m of the soil surface and divided into two equal parts of 15 m × 15 m × 2.3 m. In addition, a 12 m wide strip of land surrounding the lysimeter was reserved as border to be planted with the same crop and treated similarly. The whole area was surrounded by a 2.5 m deep trench.

In the growing season of 1983/1984, the lysimeter and the border area was planted (26 October 1983) with the two cultivars, M Col 1684 and CM 507-37 (a hybrid of M Col 1684 × M Col 1438) at a population density of 12500 plants ha^{-1}. The soil was fertilized, prior to planting, with 100, 200 and 100 kg ha^{-1} of N, P and K, respectively. Hand weeding and pesticide application were practiced whenever needed. The plots received no water other than the natural rainfall. The water stress treatment was initiated 90 days after planting by covering half of the experimental area with white plastic sheet to exclude rainfall for a period of 3 months. The stress treatment was terminated by removing the plastic sheet at 6 months after planting and the plants were allowed to recuperate during the rest of the growth cycle. Six harvests were carried out at 51, 90, 140, 182, 274 and 345 days after planting. Data of LAI, fallen leaves, total biomass and fresh root yield are presented in Figures 3, 4, 5 and 6, respectively.

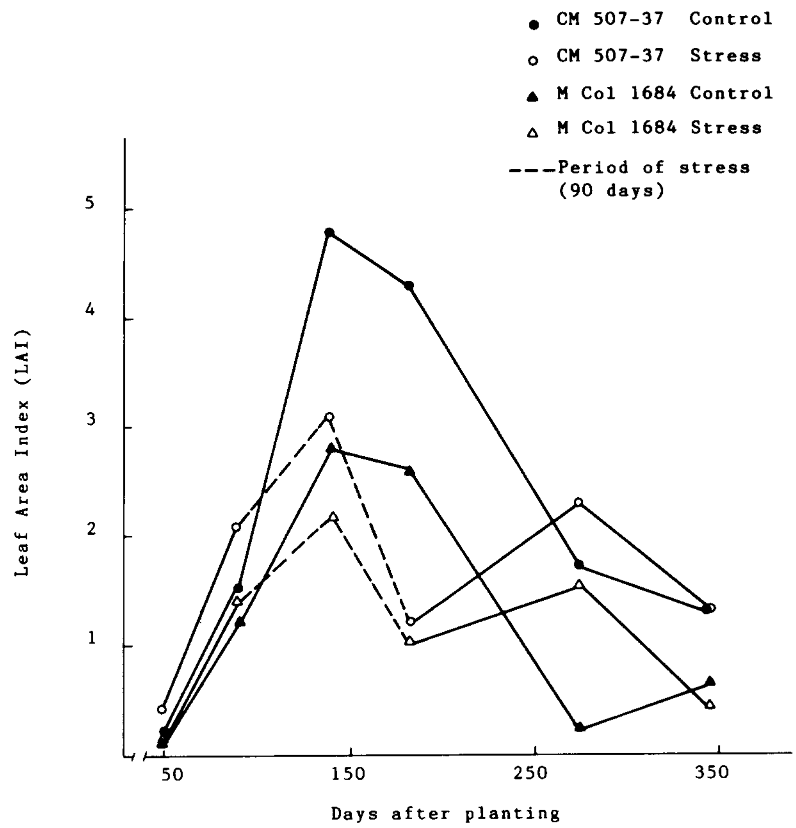

Fig. 3. Leaf area index (LAI) as a function of time after planting under nonstress and mid-term water stress conditions for the hybrid CM 507-37 and the parent M Col 1684. Rainfall was excluded by covering the soil with white plastic sheets from day 90 to day 181 after planting. (Source: CIAT, 1985).

Although cassava is highly productive under high rainfall (> 1000 mm year^{-1}), it is also highly tolerant of drought and is commonly grown in areas receiving less than 800 mm rainfall per year with a dry season of 4 to 6 months. At the onset of a dry period, the cassava crop reduces its leaf area by producing fewer and smaller leaves and shedding older leaves (See Figures 3 and 4). The reduced leaf area under dry weather could be considered a means by which cassava reduces water loss by transpiration; however, reduction in leaf area during a long period of soil water stress also reduces crop growth rate (See Figure 5). The reduction in crop growth is more pronounced in the shoots than in the roots, particularly in varieties with vigorous vegetative growth (See Table 1).

Upon recovery from water stress, cassava rapidly regenerates new leaves and the LAI of previously stressed plants becomes higher than in

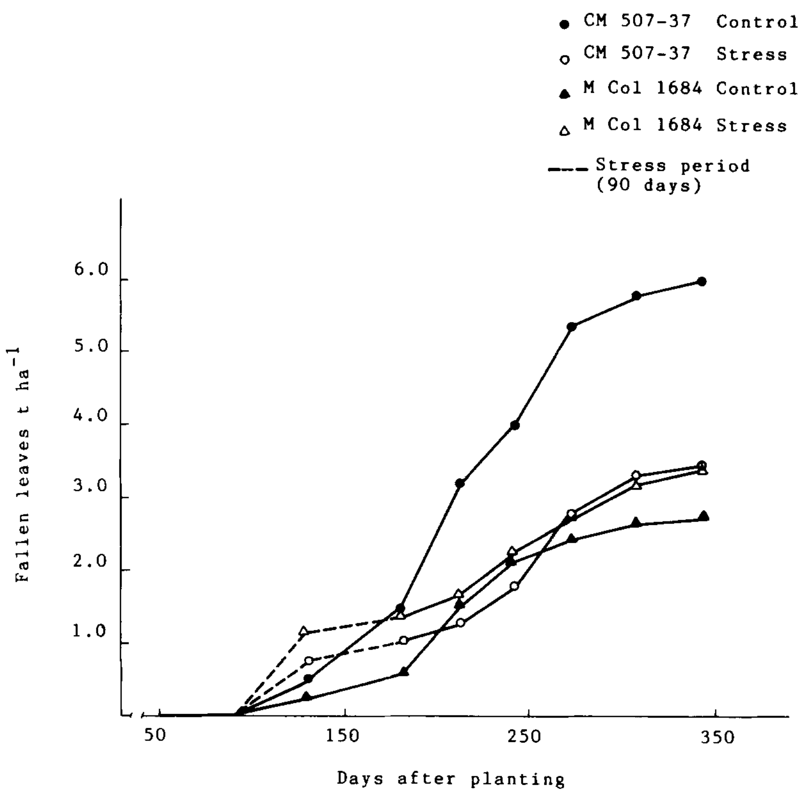

Fig. 4. Amount of fallen leaves as a function of time after planting under nonstress and mid-term water stress conditions for the hybrid MC 507-37 and the parent M Col 1684. Treatments as in Figure 3. (Source: El-Sharkawy *et al.*, unpublished).

nonstressed cassava (See Figure 3). Although the rapid production of new leaves in the stressed cassava occurs temporarily at the expense of stored carbohydrates in stems and storage roots, the increase in LAI leads to a greater accumulation of assimilates in the roots during the few months of recovery (See Figure 6). By the end of the growth cycle, the dry root yield of previously stressed cassava approaches that of the nonstressed crop (See Table 2).

IV. Discussion

Previously[1,6], it was suggested that when water stress occurs in the middle of the growth period, a vigorous variety of cassava may be preferable to a less vigorous type that may yield better under nonstress conditions. In the trials that led to this conclusion, it was not possible to ascertain whether a single plant type could yield well under both stress and nonstress conditions. The data presented in this report clearly

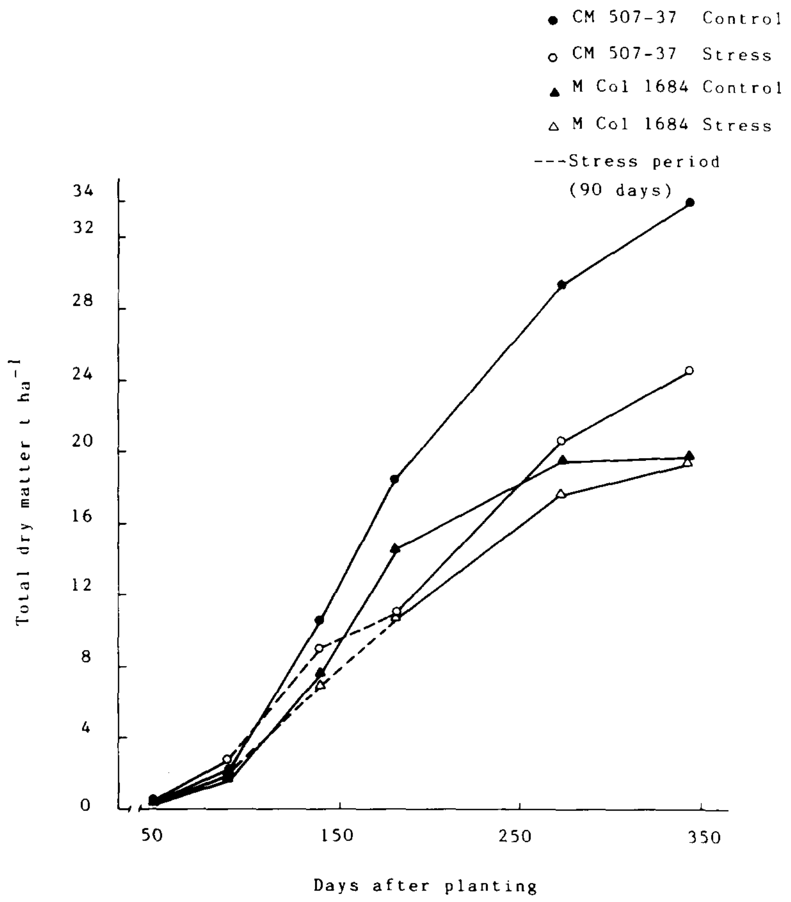

Fig. 5. Total biomass as a function of time after planting under nonstress and mid-term water stress conditions for the hybrid CM 507-37 and the parent M Col 1684. Treatments as in Figure 3. (Source: El-Sharkawy *et al.*, unpublished).

demonstrate that such a plant type does indeed exist in cassava germplasm (See Figures 3, 5, 6 and Table 2).

The hypothesis and the mechanism underlying the response of cassava to water stress are shown in Figure 7. A variety with slightly more than the optimal LAI will reduce its LAI under stress with minimal effect on yield while an optimal plant type for nonstress conditions will yield only very slightly more under these conditions, but will be very sensitive to stress. On the other hand, a variety with very large LAI will produce less under optimal conditions than under stress. It would appear, therefore, that for stable high yield in both stress and nonstress conditions, a variety with above optimal leafiness under good conditions is required. Results from field trials with several cassava varieties grown under

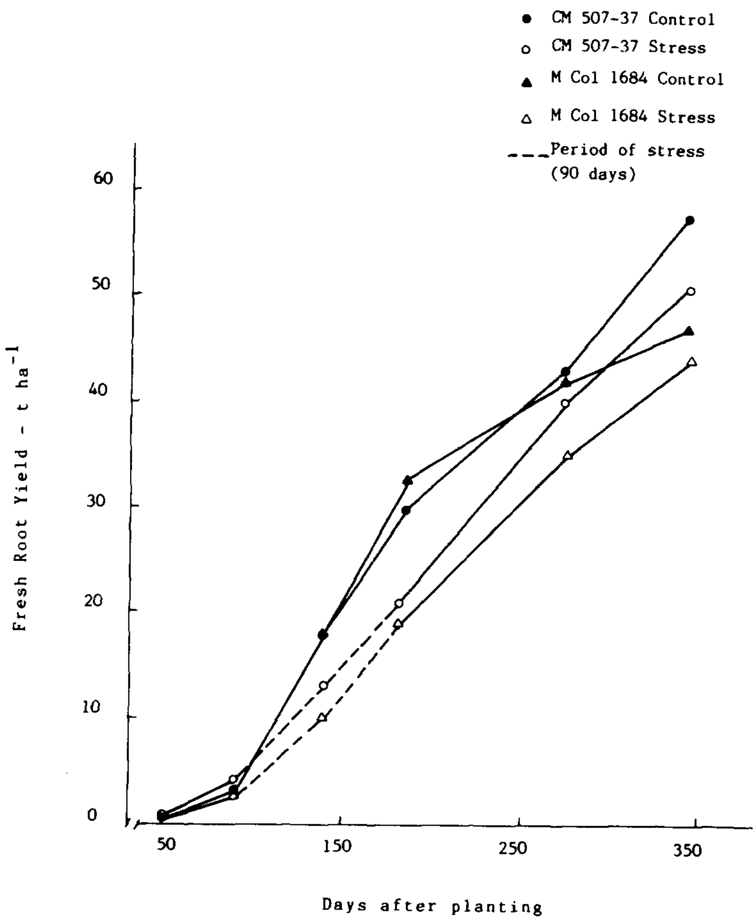

Fig. 6. Fresh root yield as a function of time after planting under nonstress and mid-term water stress conditions for the hybrid CM 507-37 and the parent M Col 1684. Treatments as in Figure 3. (Source: CIAT, 1985).

Table 1. Increase in dry roots relative to total biomass increase of four varieties, with and without water stress during the first 6 months of growth

Variety	Vegetative vigor	Period of water stress initiated at 3 months after planting (days)	Control (Dry root increase × 100) / Total biomass increase	Stressed
M Mex 59[a]	Strong	70	32	53
M Col 22[a]	Weak	70	70	87
M Col 1684	Moderate	90	77	79
CM 507-37	Moderate	90	60	80

[a] Source: Connor *et al.*, 1981.

Table 2. Total biomass and dry root yield (t/ha) of cassava at the end of the growth cycle as affected by a period of water stress during the first 6 months of growth

Variety	Period of water stress initiated at 3 months after planting (days)	Age at harvest (days)	Control		Stressed	
			Total biomass[a]	Dry root	Total biomass[a]	Dry root
M Col 1684	90	345	19.72	14.0	19.34	13.0
CM 507-37	90	345	34.0	19.0	24.4	16.0

[a] Fallen leaves are included.

natural rainfall, with and without a period of rain at the early stage of growth confirm this hypothesis[1,3].

The cultivar M Col 1684, a high-yielding, moderately vigorous type, was compared with the leafier CM 507-37 (a hybrid of M Col 1684 × M Col 1438). In the nonstressed plots, CM 507-37 reached LAIs close to five, which are above the optimum; whereas M Col 1684 scarcely reached the optimum levels of 2.5 to 3.5 (See Figure 3). In the later growth stages, the LAIs of both varieties were less than optimal, with very low levels in M Col 1684. At final harvest, CM 507-37, however, maintained significantly higher ($P < 0.01$) LAI than in M Col 1684 despite the much

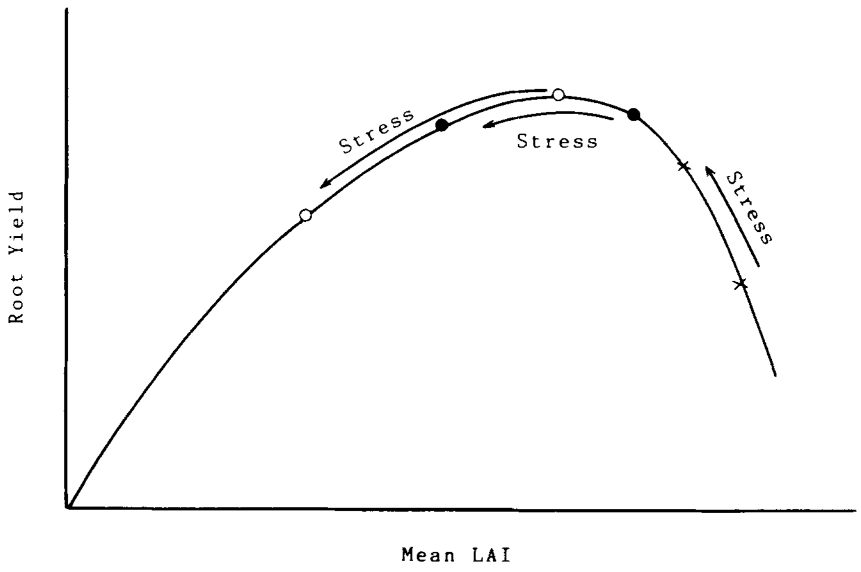

Fig. 7. Schematic diagram of how a variety can be obtained with good yield under water stress and nonstress conditions. (○ ideal plant type under ideal conditions; ● ideal plant for mid-term stress as well as ideal conditions; × excessively vigorous type, yields better under stress). (Source: CIAT, 1985).

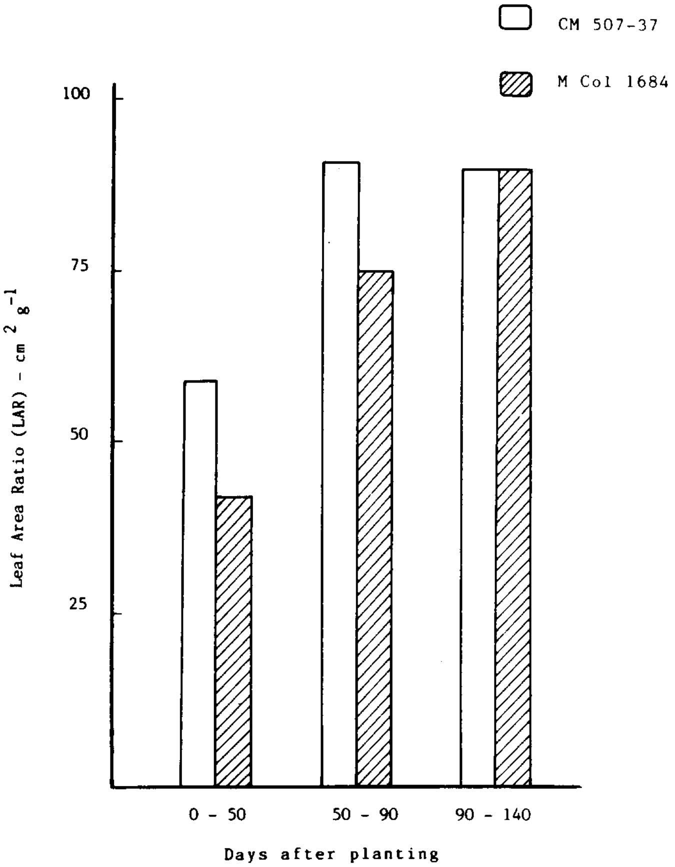

Fig. 8. Leaf area ratio (LAR) in the early growth stage of the hybrid CM 507-37 and the parent M Col 1684. Nonstressed plants. (Source: CIAT, 1985). LAR = leaf area in $cm^2 g^{-1}$ dry weight of stems + leaves.

greater fallen leaves in the former. Both fresh and dry (data not shown for the latter) root yields reflect these trends (See Figure 6). Maximum root growth rates occurred when LAIs were between 2 to 5. When the LAI of M Col 1684 dropped during the last 100 days of the growth cycle, root filling essentially ceased. CM 507-37 maintained an LAI of about 1.5 during this period and substantially outyielded M Col 1684 as a result. The question still remains as to why the early yield (*e.g.*, at six months after planting) of CM 507-37 with an above-optimum LAI was equal to that of M Col 1684. The leaf area ratio (LAR), calculated only for the aboveground portions of the plant, was greater in CM 507-37 than that of M Col 1684 (See Figure 8). This indicates that CM 507-37 used dry matter in the aerial portion of the plant more effectively for producing leaves than M Col 1684, resulting in a higher optimal LAI.

This is presumably related to smaller nodes and internodes per unit leaf area in CM 507-37.

In the stressed plots, the LAIs, total biomass and storage root yields were all significantly reduced ($P < 0.01$) in both varieties after 90 days without rain (see Figures 3, 5 and 6). Compared with the nonstressed plots at 6 months after planting, the percentage decreases in LAI, total biomass, fresh and dry root yields were 61.5, 26.7, 42.4 and 36.4 in M Col 1684, and 72.1, 41.2, 30.0 and 31.6 in CM 507-37. It is apparent, therefore, that in CM 507-37, reductions were greater in LAI and total biomass as compared with M Col 1684. On the other hand, reductions in fresh and dry root yields were greater in M Col 1684. The total biomass and root yields at 6 months after planting were similar for both varieties. CM 507-37, however, maintained significantly higher ($P < 0.01$) LAI during the stress period. This can be attributed, partially, to the ability of the hybrid CM 507-37 to retain its leaves much longer since its fallen leaves were less than in M Col 1684 (See Figure 4). Furthermore, CM 507-37 produced a flush of new leaves during the recovery period and thus maintained a higher LAI, up to the final harvest, than M Col 1684. By the end of the growth cycle, the amount of fallen leaves were the same in both varieties. The significantly higher ($P < 0.05$) LAI of CM 507-37 during the recovery period presumably resulted in significantly higher ($P < 0.05$) root yield at the final harvest (19.3 and 23.1% increases in fresh and dry roots above M Col 1684) (See Figure 6 and Table 2). The same trend existed in final total biomass (26.2% increase above M Col 1684, $P < 0.05$).

Compared with the nonstressed plots, the reduction in dry root yield at the final harvest of M Col 1684 was slight (7.1%) probably because of the large increase in LAI during the recovery period and also because of the lack of root yield increase in the control during the last two months of growth. Similarly, the final total biomass was not different between the two treatments (See Figure 5 and Table 2). On the other hand, the reductions, due to mid – term water stress, in final dry root yield (15.8%) and total biomass (28.2%) in CM 507-37 were significant ($P < 0.05$). Nevertheless, reduction in total biomass in CM 507-37 was substantially greater than reduction in root yield indicating a larger partitioning of assimilates into the roots in this case. This conclusion is further supported by the higher final harvest index (percent dry root to total biomass) in the stressed plots (66%) as compared with the nonstressed plots (56%) (See Table 2). It appears, therefore, that the favorable partitioning of assimilates into the roots that was induced by mid – term water stress (See Table 1) persisted through the recovering period.

The paramount importance of LAI in determining yield even when a long stress period occurs is shown in Figure 9. The yield of four cultivars,

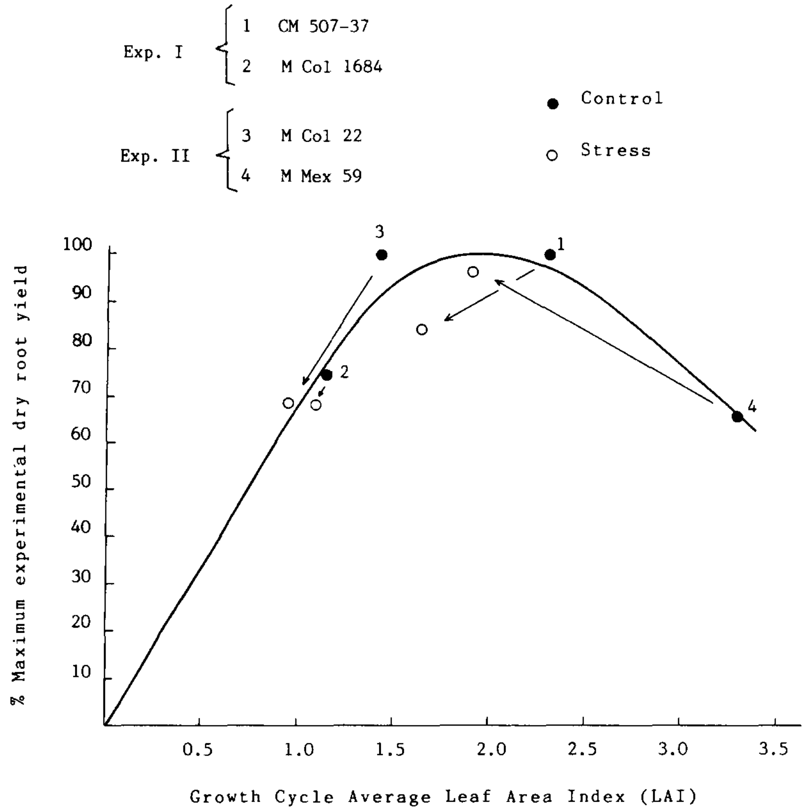

Fig. 9. Dry root yield as a function of growth cycle average leaf area index (LAI) under nonstress and mid—-term water stress conditions for 4 cultivars with different vigors. (Data of experiment I for CM 507-37 and M Col 1684, from El-Sharkawy *et al.*, unpublished; data of experiment II for M Col 22 and M Mex 59, from Connor *et al.*, 1981).

different in their vigor and grown under nonstress and mid—term stress conditions in two separate trials, is closely associated with the average LAI during the growth cycle (LAI is a characteristic of the genotype and is also highly dependent on water conditions). The highest reference (100%) yields in both trials were 19 t dry root ha^{-1} for CM 507-37 under nonstress conditions over 345 days (Experiment I) and 11.2 t ha^{-1} for M Col 22 under nonstress conditions over 306 days (Experiment II). It is apparent that the performance of these cultivars conforms to the suggested hypothesis.

Finally, it is of interest here to comment on another plant characteristic of importance in the soil-water-plant relationship; *i.e.*, the fibrous root system[2,15]. Table 3 summarizes data concerning the characteristics of the fibrous root system and soil water profile of six—month—old, field—grown plants of M Col 1684 and CM 507-37. The two cultivars

Table 3. Characteristics of fibrous root system and soil water profile of six–month–old field–grown plants of cassava cultivars M Col 1684 and CM 507-37; planted on April 15 and sampled on October 15, 1983, at Santander de Quilichao, Colombia. Soil cores (390 cm^3) were taken by hand augor for determination of root characteristics and soil water content. Values are means of 4 profiles

Soil layer (m)	M Col 1684			CM 507-37		
	Root length density ($cm\,cm^{-3}$)	Root diameter (mm)	Soil water (% vol)	Root length density ($cm\,cm^{-3}$)	Root diameter (mm)	Soil water (% vol)
0.2	0.454	0.970	25.6	0.715	0.520	26.9
0.4	0.189	0.923	39.2	0.195	0.576	37.3
0.6	0.128	0.688	50.2	0.129	0.727	48.8
0.8	0.069	0.670	54.7	0.068	0.553	55.5
1.0	0.051	0.715	58.7	0.068	0.481	58.6
1.2	0.051	0.634	61.5	0.057	0.488	60.5
1.4	–	–	65.2	0.026	0.504	62.7
1.6	–	–	69.0	0.051	0.532	63.3
1.8	–	–	69.0	0.054	0.554	63.3
2.0	–	–	–	0.059	0.536	–

were planted in the same field for commercial production on April 15, 1983, at the CIAT experimental station in Santander de Quilichao, Colombia, and received no water other than natural rainfall. The summer that year was exceptionally dry; from the beginning of June, when the plants were only 45 days old, to the first week of October (130 days), the total amount of rainfall was 180 mm. This amount of rainfall fell far below the potential evaporation (4.4 mm day^{-1}). From the time of planting (April 15) to the end of May, the rainfall was 390 mm, for a total of 570 mm in the first six months of growth[2]. At this age, the total biomass of the hybrid CM 507-37 was 19% greater than that of M Col 1684 (8.0 *vs.* 6.7 t ha^{-1})[2]. Dry root yield was the same in both cultivars (3.6 and 3.7 t ha^{-1} for CM 507-37 and M Col 1684, respectively). CM 507-37, however, maintained a higher LAI (1.1 as compared with 0.4 for M Col 1684).

These differences in growth and biomass production under naturally stressful environmental conditions were apparently associated with differences in characteristics of fibrous root system and in patterns of soil water depletion (See Table 3). The hybrid CM 507-37 had a finer and more concentrated root density in the upper layer of soil and its root system penetrated into deeper soil layers (perhaps below the 2 meter depth) than M Col 1684. The more intensive and extensive root system of CM 507-37 was advantageous in terms of its ability to withdraw more water (and perhaps more nutrients) from larger and deeper volumes of soil. This might explain, at least partially, the higher leaf area and the greater biomass production by CM 507-37 under severe and prolonged soil-water stress. Varietal differences in rooting characteristics at an early

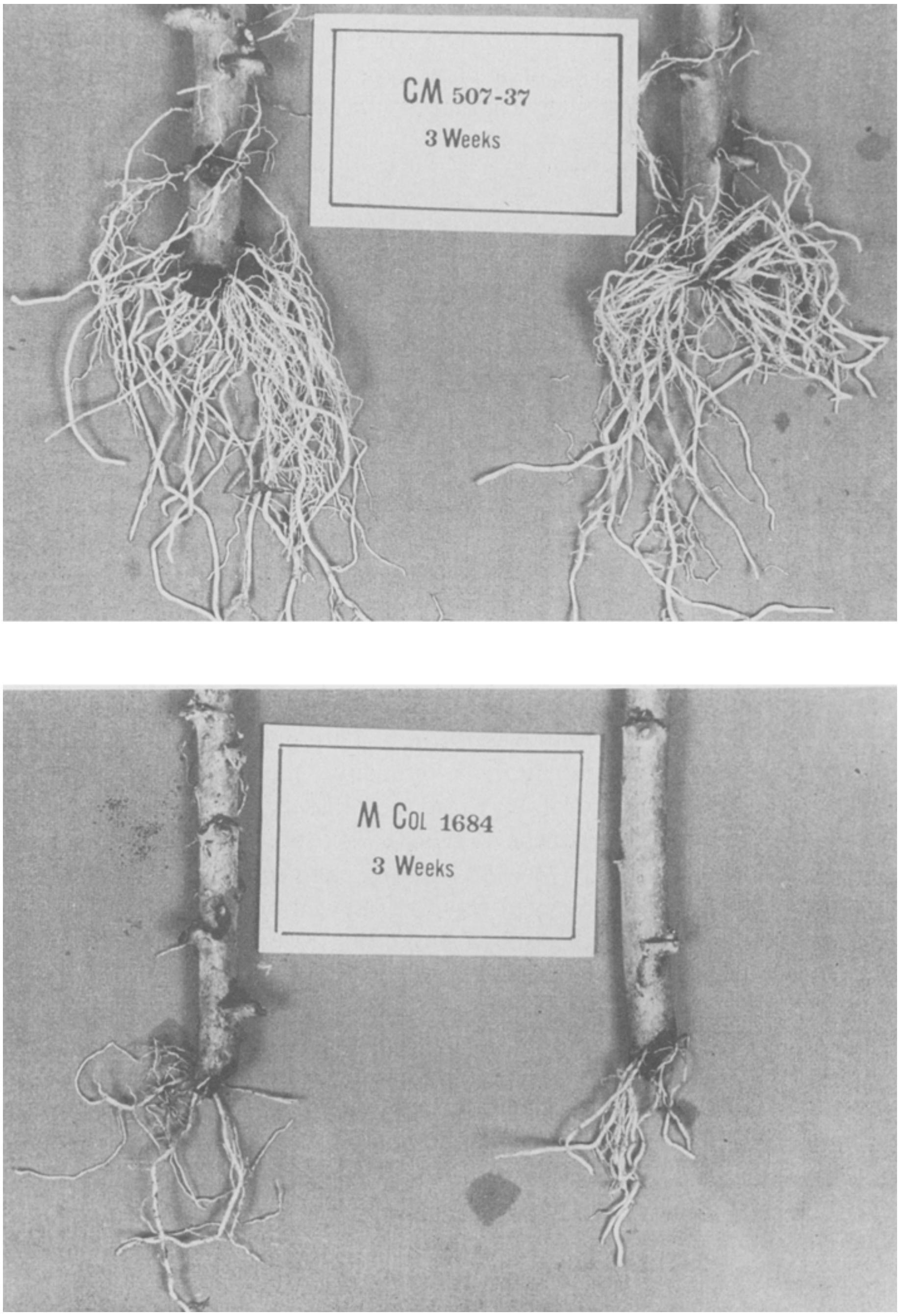

Fig. 10. Rooting characteristics at three weeks after planting of stem cuttings of the hybrid CM 507-37 and the parent M Col 1684 (Source: El-Sharkawy *et al.*, unpublished).

stage were sought, and it was found that CM 507-37 rooted better within the first three weeks of germination (Figure 10). It is possible, therefore, to breed and select for cassava plant types that perform well in both stressful and nonstressful environments, by combining desirable characteristics of leaves and roots.

In conclusion, it can be stated that high yield under mid – term stress conditions is not incompatible with high yield under nonstress conditions. The high yield levels under both conditions (*e.g.*, CM 507-37 with dry root yield of 16 and 19 t ha^{-1} in less than one year, with and without stress) can be obtained by having slightly higher than optimal LAI under nonstress conditions. The extra "energy cost" required for obtaining this type of plant appears to be associated with diverting more dry matter into an extensive fibrous root system. With regard to partitioning dry matter to a fibrous root system, cassava can generally be considered a conservative crop in comparison with other crop species[13,17].

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