

The Physiology section has shifted emphasis from the ideal plant type for near ideal conditions towards identifying which characters are associated with high root yield and quality under stress conditions. Work in 1980 was directed to a detailed study of the plant's reaction to water stress.

Growth and Yield under Water Stress

Growth and yields of the vigorous (M Mex 59) and the low-vigor cassava variety (M Col 22) were studied with a period of artificial rain exclusion. Stress was obtained by covering the soil with plastic from 15 to 25 weeks after planting; control plots received the natural rainfall which was well distributed and totaled about 500 mm during the 10-week period. Due to a natural dry period (approximately 120 mm of rain during 11 weeks) just before the exclusion period, plots were already stressed before the treatment period. Plant growth and development were followed throughout the stress period and subsequent recovery.

Control plots of M Mex 59 were extremely vigorous with leaf area indices (LAI) above three for much of the growth period and above four for considerable periods (Fig. 1). These LAI values are well above the normal optimum of 2.5-3.5 for root yield. Control plots of M Col 22 never attained LAIs higher than three and were suboptimal for most of the growth period. In both varieties, water stress reduced LAIs markedly, although M Mex 59 maintained a LAI approximately twice that of M Col 22 during the stress period.

Changes in LAIs are determined by the initial LAI, the number and leaf area of leaves formed, and the area of fallen leaves. The decrease in LAI during water stress periods is frequently said to be due to increased leaf fall. In this experiment total leaf fall in the stress period was reduced in the stress plots (Fig. 2,a and b). Mean age of fallen leaves from M Col 22 was similar in control and stressed plants (Fig. 2,a). In M Mex 59, leaf life was

slightly longer in stressed plots due to reduced shading of lower leaves which resulted from decreased leaf area production (Fig. 2,b).

Reduced leaf area during stress was due to reduced production of new leaves and reduced leaf size (Fig. 2,c). In turn, the decreased number of new leaves was due to both reduced branching (Fig. 3,a) and reduced leaf formation per apex (Fig. 3,b). Work with pot plants suggests that leaf expansion and, hence, leaf size are extremely sensitive to water stress.

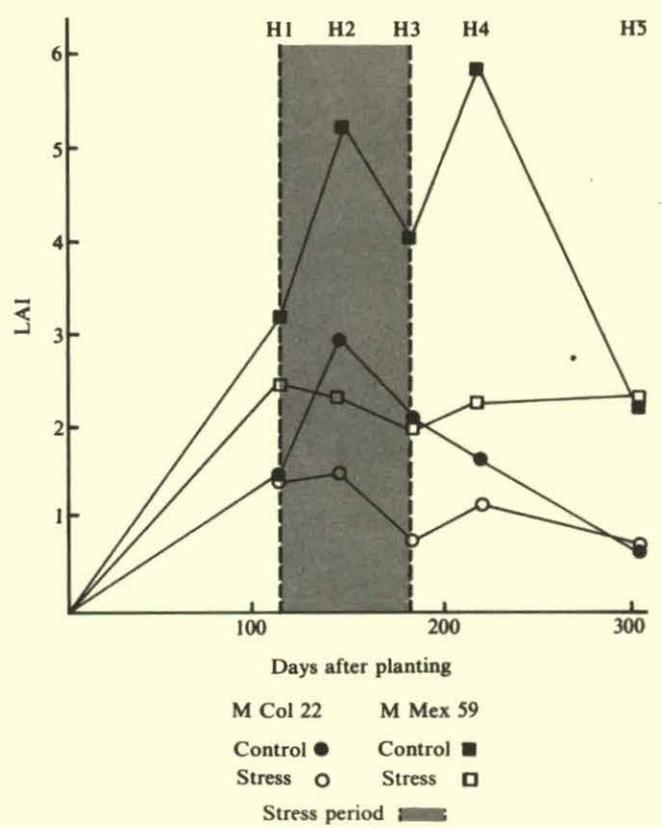


Figure 1. Leaf area indices (LAI) of cassava cultivars M Mex 59 and M Col 22 during and after a water stress period. H = harvest.

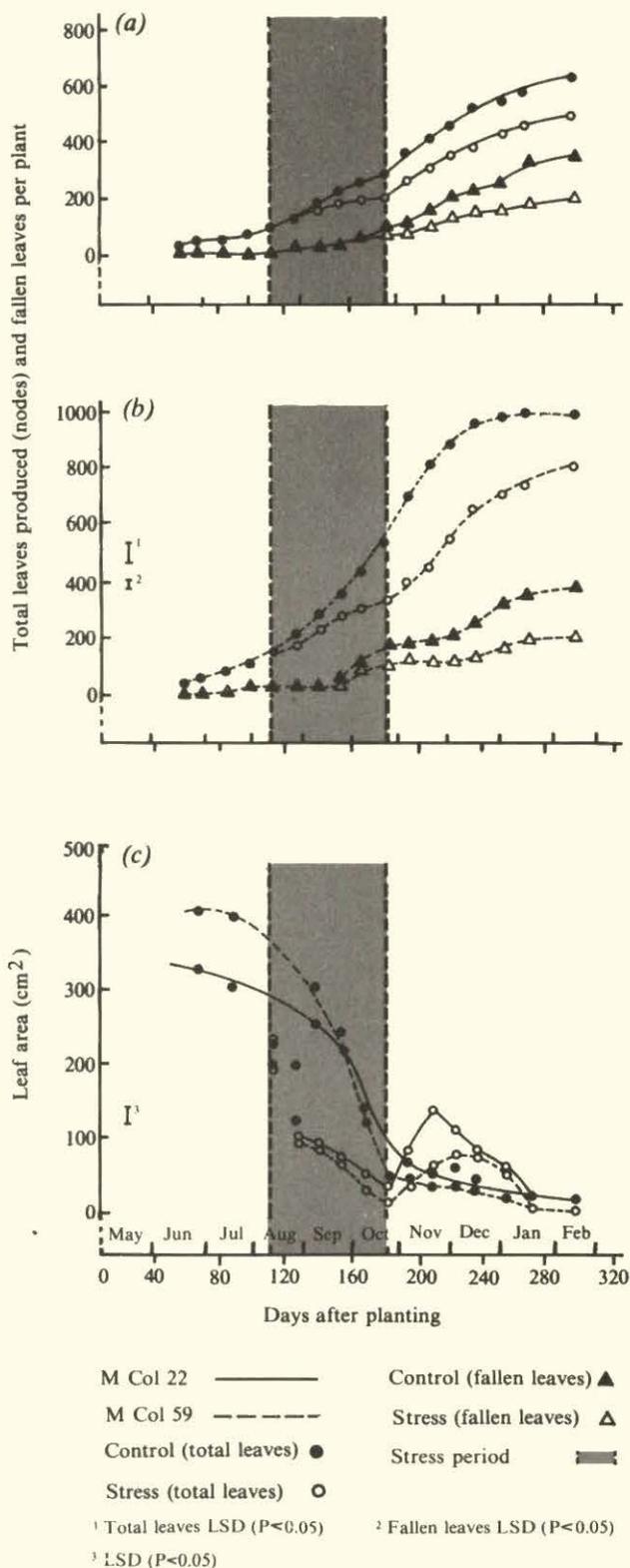


Figure 2. Leaf production and leaf fall (a and b) and leaf size (c) of two cassava cultivars during and after a water stress period.

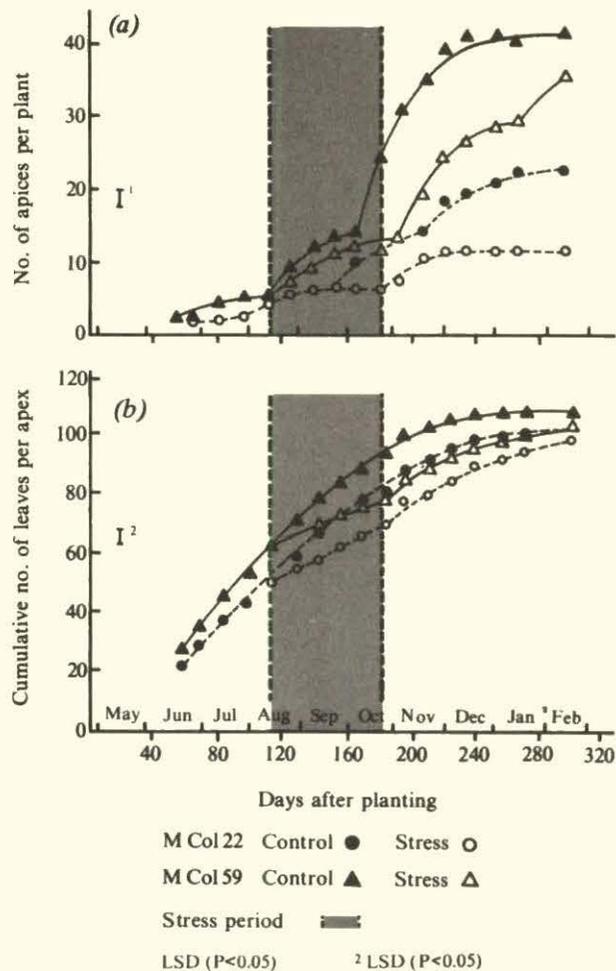


Figure 3. Number of apices (a) and cumulative number of leaves per apex (b) of two cassava cultivars during and after a water stress period.

The reduction in LAI and stomatal closure during the stress period caused a marked decrease in crop growth rate (Table 1). However, the percentage increase in standing biomass found in the roots greatly increased in the stressed plots, from 32 to 53% in M Mex 59 and from 70 to 87% in M Col 22. A direct result of this was that root yield of M Mex 59 was not significantly reduced in the stress period (Fig. 4) and that root yield was reduced proportionately less than crop growth in both varieties. Thus, during stress the crop tends to maintain root growth at the expense of top growth, utilizing reduced dry matter production extremely efficiently.

The marked decrease in LAI during the stress period is a mechanism to reduce transpiration (i.e., water loss) although loss of water was also controlled by stomatal closure. Leaves of plants in stressed plots had consistently

lower leaf conductance (a measure of stomatal opening) than did control plants. Leaf conductance of M Mex 59 was somewhat less than that of M Col 22, however, calculations suggested that total transpiration was similar due to the greater LAI of M Mex 59. Stomatal control was such that leaf water potential remained at similar levels in both stressed and control plots. The minimum leaf water potentials were approximately -1.5 MPa in both varieties.

Table 1. Crop growth rate of cassava cultivars M Col 22 and M Mex 59 during and after a water stress period.

Period ¹	Duration (days)	Mean daily solar irradiance (MJ/m ²)	Mean growth rate (kg/ha per day)			
			M Col 22		M Mex 59	
			Control	Stress	Control	Stress
PD - H1	109	17.3	27	27	39	30
H1 - H2	39	18.2	103	62	96	47
H2 - H3	33	19.3	112	14	74	51
H3 - H4	38	19.7	113	40	130	31
H4 - H5	87	20.3	17	35	61	115

¹ H = harvest; PD = Planting date

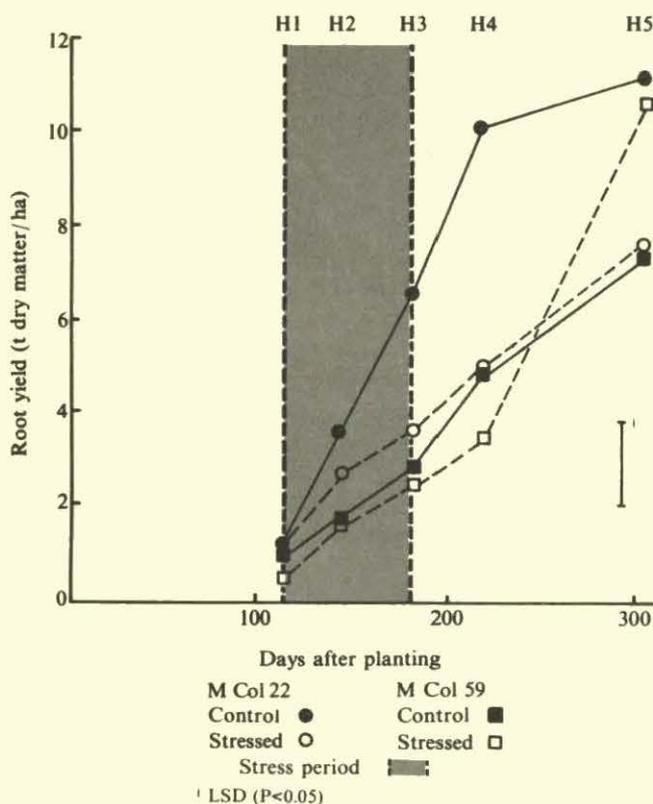


Figure 4. Dry root yields of two cassava cultivars during and after a water stress period. H = harvest.

Both varieties also reduced average soil water potential to a depth of 2 m (maximum depth measured) to about -1.5 MPa, a level similar to that of the leaves. Soil water decreases were similar in both varieties, again suggesting similar transpiration rates for both varieties even with large differences in LAI.

At the second harvest, in the middle of the stress period, stressed plants of M Mex 59 had significantly more roots at greater depth than the controls. By the fourth harvest, roots were found 2.6 m deep, the greatest depth sampled. Although the cassava root system was quite deep it was also relatively sparse compared to many other crop plants. This rather sparse root system may well be a mechanism that leads to slow water use under drought and allows rather low levels of transpiration and growth to continue.

These data suggest that during a stress period the cassava plant can extract soil water to a depth of at least 2 m, to soil water potentials of -1.5 MPa. The sparse root system, reduced leaf area and partial stomatal closure all lead to a slow but prolonged water uptake during a stress period allowing continued but rather slow total growth. At the same time, the proportion of total growth used in root expansion increases under stress enabling the plant to minimize the reduction in root growth. This effect was particularly noticeable in the more vigorous variety M Mex 59.

After the stress period, a flush of new growth appeared. Pot trials show that leaves that pass through the stress period rapidly increase their photosynthetic rates when rewatered (Fig. 5), providing the plant with a positive carbon balance as soon as water becomes available. Root reserves are also apparently used for rapid regrowth of the tops (see next section). Leaf area indices in both varieties increased during recuperation, and by final harvest 10 months after planting, were similar in both control and stressed plants (Fig. 1).

Leaf area recovery was related to leaf formation rate per apex and branching; leaf formation rate per plant was similar in recuperating and control plants (Fig. 2). Leaves of recuperating plants were, however, much larger than those of the controls at similar node levels. Large leaf size during early recuperation allowed plants to rapidly increase LAI.

Total nodes produced in stressed plants were always less than in unstressed plants so stem weight increases were less in the former during recovery. LAI in M Mex 59 was sufficient to achieve reasonable daily growth rates of 89.5 kg/ha in recuperating plants, compared to 82.0 kg/ha in

controls; this coupled with decreased stem growth resulted in greater final yield (10.7 t dry roots/ha) in stressed plants than in the controls (7.6 t/ha). On the other hand, the LAI of previously stressed M Col 22 was so low that daily growth was reduced markedly (36.5 kg/ha) compared to the controls (46.2 kg/ha) and root growth rate was lower during recovery leading to a yield of 7.3 t/ha in the stressed plots compared to 11.2 t/ha in the controls.

These results suggest that when stress occurs in the middle of the growth period, a vigorous cassava variety may be preferable to a less vigorous type which may yield better under non-stress conditions.

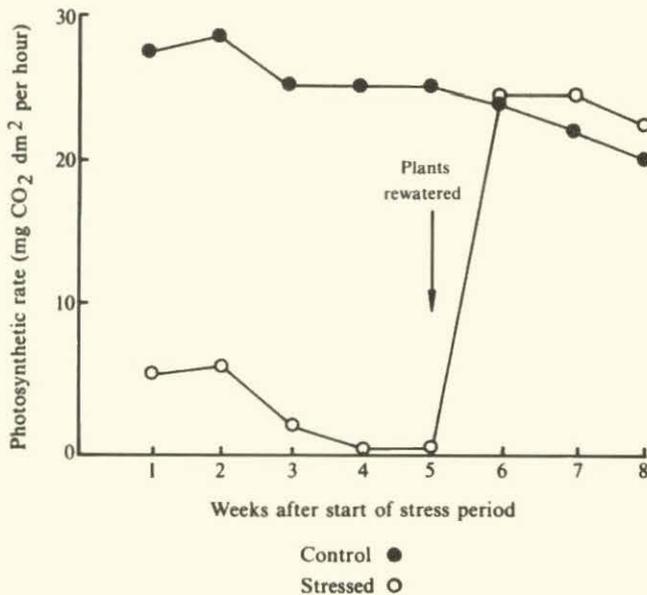


Figure 5. Photosynthetic rate of the same leaf of pot-grown plants of cassava cultivar M Col 1684 during and after a water stress period.

Root Quality under Water Stress

Root quality of cassava is closely related to dry matter content and starch content. Dry matter content of control plants in the experiment described above increased steadily with age of the crop until the final harvest 10 months after planting. Root dry matter of M Col 22 increased markedly during the first part of the stress period (Fig. 6); however, during recuperation, there was a marked decrease in dry matter that was maintained to a lesser extent by final harvest. This decrease in dry matter in the recuperation phase is consistent with the hypothesis that root reserves are used to produce the rapid flush of growth during recuperation.

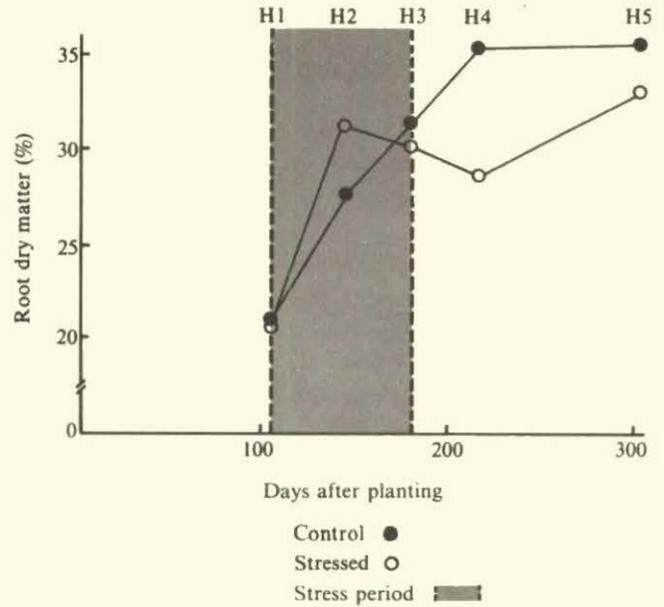


Figure 6. Changes in root dry matter of cassava cultivar M Col 22 during and after a water stress period. H = harvest.

Starch content increased slightly by the end of the stress period (20.1 versus 18.3%). However, by the end of the first recuperation phase starch content had risen to only 20.3% compared to 26.3% in the controls and this difference still existed at a reduced level by final harvest. Starch content (root quality) was, therefore, most affected by stress in the recuperation phase and was never completely recovered.

Growth Analysis

During recent years the clone M Col 1684 has consistently been one of the highest yielding varieties over a wide range of conditions in the regional trials network. Growth and development of M Col 1684 were compared to M Ven 77, M Ptr 26 and M Col 22 at CIAT-Palmira to determine if basic differences existed between M Col 1684 and the other clones. At final harvest one year after planting, yields ranged from 10.4 t dry roots/ha in M Ven 77 to 14.4 t dry roots/ha in M Col 1684. Total biomass (including fallen leaves) varied little (26.1-27.4 t dry matter/ha) and, hence, yield differences were mainly due to differences in harvest index, which ranged from 0.40 in M Ven 77 to 0.53 in M Col 1684.

The pattern of leaf area development in all varieties was similar, although M Col 22 developed more slowly but maintained a higher LAI during later growth stages.

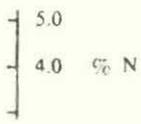
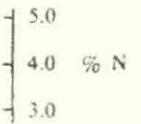
M Col 1684 was by far the most profuse branching of the four clones tested. Whereas branch number of the other varieties increased in a phasic manner, the number of active apices of M Col 1684 fluctuated widely. These fluctuations are not due to a large variability in the data but, rather, due to a high mortality rate of apices at certain times. Apex mortality under stress conditions may allow M Col 1684 to rapidly adjust its leaf area to stress conditions and this dieback may reduce the amount of dry matter required for node growth in the recovery phase.

Although early branching was much greater in M Col 1684, its LAI did not tend to be greater than that of the other lines due to a small maximum leaf size, a very early

decline in leaf size with plant age, and a relatively low leaf formation rate per apex.

Other characters such as photosynthetic rate, water use efficiency of single leaves, root number, leaf inclination and the relation between crop growth rate and LAI showed no major differences that could be associated with higher yield in M Col 1684.

Errata

Page	Column	Element	Printed:	Should be:
6	1	Figure 2	M Col 59	M Mex 59
6	2	Figure 3	M Col 59	M Mex 59
6	2	Figure 3	LSD ($P < 0.05$)	LSD ($P < 0.05$)
7	1	Figure 4	M Col 59	M Mex 59
60	2	Second para., line 8	more to growth	more top growth
61	2	Line 1	and K contents	and K concentrations
20	1	Figure 1	I - Tolerant III - Tolerant V - Tolerant	I - Intermediate-resistant III - Intermediate-resistant V - Intermediate-resistant
62	1	Figure 3	Stems □	Stems △
64	1	Figure 5		
66	1	Figure 8	Figure 44	Figure 8
93	2	Footnote	*Left during 1979.	*Left during 1980.