PHOTOSYNTHETICA 34 (2): 233-239, 1997

Response of cassava (*Manihot esculenta* Crantz) to water stress and fertilization*

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Abstract

Experiments done in Santander de Quilichao (Cauca, Colombia) on two cassava cultivars indicated that cassava had at least three defence mechanisms against water deficit, enabling it to assimilate and store photosynthates in roots, even during prolonged droughts. These mechanisms include partial stomatal closure, ability of leaves to maintain reasonable net photosynthetic rate for long periods of water stress, reduced leaf area, and exploration of water from deep soil layers. While cassava responded positively to fertilization, no significant statistical differences were found between treatments of stress and non-stress, confirming cassava's ability to tolerate soil water deficit.

Additional key words: dry matter production; leaf area index; photosynthetic rate; water deficit; water potential.

Introduction

Cassava, a native to tropical America, is a woody shrub belonging to the *Euphorbiaceae* family. Cassava is a highly efficient starch producer, and its outstanding feature is ability to produce biomass in areas with acid and infertile soils, and under prolonged droughts (Cock and Howeler 1978, Howeler and Cadavid 1983, Cock *et al.* 1985, El-Sharkawy and Cock 1987, Ramanujam 1990, El-Sharkawy *et al.* 1992b, El-Sharkawy 1993). Its photosynthetic capacity is a major determinant of productivity (Cock and El-Sharkawy 1988, El-Sharkawy *et al.* 1990, 1993). Studies carried out by El-Sharkawy *et al.* (1990) and by de Tafur *et al.* (1997) showed positive and significant correlations between root production, fresh biomass, and photosynthetic rate.

This work aims at evaluating the physiological response of cassava to the interactions between water stress and fertilization, and their effects on yield.

Received 25 June 1996, *accepted* 16 August 1996.

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This work is part of a M.S. Thesis by S.M. de T., Facultad de Ciencias Agropecurias, Universidad Nacional de Colombia, Palmira, Valle, Colombia 1994.

Materials and methods

The trial was carried out in the 1993/1994 season at the experiment station of the International Centre for Tropical Agriculture in Santander de Quilichao (Cauca, Colombia, lat. 3°6'N, 76°31'W, altitude 990 m). Average temperature, rainfall, and relative humidity were 23.8 °C, 1769 mm, and 74 %, respectively. During the first 3 months after planting (March to May 1993), rainfall was much higher than pan evaporation (> 5 mm d^{-1}) which had led to excess drainage water. Although the soil (oxisols) has a high organic matter content, it has extremely low concentrations of P, low concentrations of Ca, Mg, and B, and only moderate concentrations of K. The cultivars M Col 1684 and CM 507-37, from the CIAT-Palmira collection, were planted on ridges at a density of 1 plant m^{-2} on March 3, 1993.

Water stress was induced 4 months after planting, and was maintained up to the final harvest by covering the ground with white, caliber 6 plastic. A split-split plot design with four replications was used. The main plot corresponded to stress treatment, the subplots to cultivars, and the sub-subplots to fertilization (with 5.0, 4.4, and 8.3 g m^{-2} of N, P and K, respectively, or without). During drought, the non-stressed plots received weekly irrigation of 20 mm to supplement rainfall between July to October 1993 when precipitation was less than pan evaporation (< 4 mm d^{-1}). Four sequential harvests, conducted at 3, 5, 7, and 12 months after planting, yielded results on dry matter production and root yield, excluding fallen leaves and fine roots. Six guarded plants were harvested per plot, and separated to storage roots, stems, and leaves. After determining their fresh mass, they were oven-dried at 60 °C for 48 h. Soil moisture in the stressed plots was assessed by the gravimetric method.

Net photosynthetic rate (P_N) was determined with an *LCA-2* portable (*Analytical Development Co.*, Hoddesdon, England) system, which consisted of an air pump, infrared gas analyzer (IRGA), data logger, and Parkinson Broad Leaf Model chamber. The P_N was measured on mature upper canopy leaves using atmospheric air [340 μmol(CO_2) mol^{-1}(air)] under a solar irradiance higher than 1000 μmol m^{-2} s^{-1} between 08:00-12:00 h, and calculated according to Coombs *et al.* (1988).

Leaf area index (LAI) was measured using an *LAI-2000* Plant Canopy Analyzer (*LICOR*, Lincoln, Nebraska, U.S.A.) that computed LAI from radiation interception. The radiation interception was measured from five locations within each plot between 08:00-10:00 h.

Leaf water potential was determined with a *3005* Plant Water Status Console Pressure chamber (*Soil Moisture Equipment Corp.*, Santa Barbara, CA, U.S.A.) using compressed nitrogen. Before leaves were detached, they were enclosed in small plastic bags that had a small wet towel in order to minimize water loss from leaves before measurements.

Results and discussion

Water absorption pattern under stress (Fig. 1) in cultivars M Col 1684 and CM 507 37, with and without fertilization, indicated that these plants extracted larger amounts of water from the upper soil layers during the first 24 d of stress. As the surface soil layers became dry, the plants extracted water from the deeper layers. Cassava can extend its fibrous roots to 2 m or more in depth, and thus absorb water from deeper strata of the profile during drought periods (Connor *et al.* 1981, El-Sharkawy *et al.* 1992a).

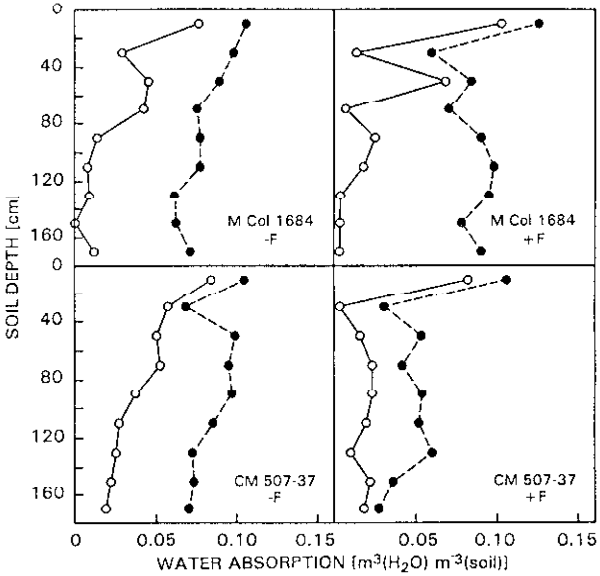

Fig. 1. Water absorption patterns in two cassava cultivars (M Col 1684, CM 507-37) 24 (○) and 160 (●) d after the start of stress treatments, with (+F) or without (-F) fertilization.

Table 1. Total dry biomass production [kg m^{-2}] at harvest of two cassava cultivars with (+) and without (-) water stress (WS) and with (+) and without (-) fertilization (F), determined 3, 5, 7, and 12 months after planting. Values within columns followed by the same letter(s) are not significantly different ($p < 0.05$).

Cultivar	WS	F	Dry biomass			
			3	5	7	12
M Col 1684	+	+	0.082 a	0.328 a	0.424 b	0.880 a
M Col 1684	+	-	0.037 b	0.191 cd	0.252 c	0.569 b
M Col 1684	-	+	0.036 b	0.230 bc	0.436 b	0.906 a
M Col 1684	-	-	0.020 cd	0.146 d	0.236 c	0.312 c
CM 507-37	+	+	0.087 a	0.354 a	0.372 b	0.828 a
CM 507-37	+	-	0.042 b	0.213 bc	0.248 c	0.531 bc
CM 507-37	-	+	0.032 bc	0.250 b	0.715 a	0.869 a
CM 507-37	-	-	0.014 d	0.152 d	0.433 b	0.416 bc

Dry matter production: In the first and second harvests, stress and fertilization had positive effects (Table 1). The same occurred in the third harvest, with significant differences between cultivars in the production of total dry biomass: thus, CM 507-37 gave higher yields in absence of water stress than M Col 1684. The fourth harvest, 12 months after planting, did not present significant differences between the stress and non-stress treatments nor between cultivars, but, as in the previous samplings, response to fertilizer application was highly significant.

In general, dry matter production in roots and stems increased over time, whereas dry matter production in leaves decreased after the month 7 in the non-stress treatment, and at the beginning of the same month in the stress treatment.

Photosynthesis: The first four P_N readings did not show significant differences between water stress and non-stress treatments (Fig. 2). Nor were differences found between the fertilized and unfertilized treatments, but a highly significant difference was found between the two cultivars, and CM 507-37 achieved the highest P_N.

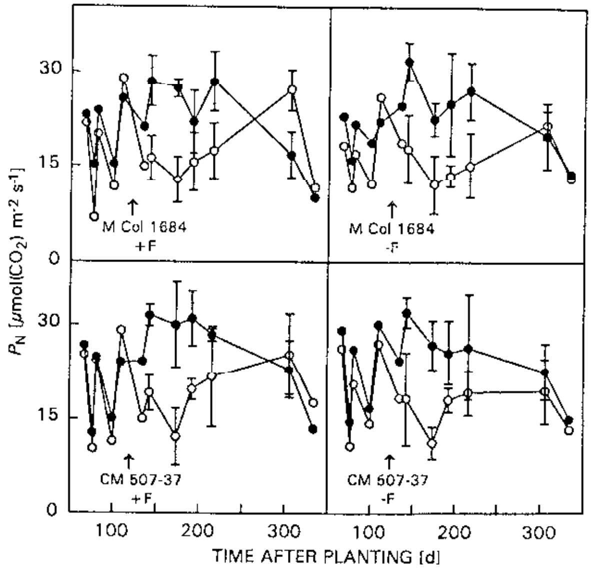

Fig. 2. Net photosynthetic rate (P_N) in two cassava cultivars (M Col 1684, CM 507-37) throughout the experiment, with (○) or without (●) stress, with (+F) or without (-F) fertilization. ↑ indicates the initiation of water stress. Bars ± sd.

120 d after planting when water stress was induced, highly significant differences occurred between stress and non-stress treatments, with means of 15.8 and 25.7 μmol(CO$_2$) m^{-2} s^{-1}, respectively. Yet 300 d after planting, no significant differences occurred between treatments, possibly because of plant age and root-sink limitation. The crop was 11 and 12 months old, respectively, stages at which new leaves are not formed and storage roots are already filled with starch. Yet average P_N values in young leaves formed after the induction of water stress were similar throughout treatments but significantly different from those of old leaves under stress (Table 2).

These results confirm that cassava tolerates soil water deficit well, even during prolonged periods. Although the P_N decreases significantly, leaves continue to produce photosynthates that are stored in the roots.

Table 2. Average net photosynthetic rates, P_N [μmol(CO$_2$) m^{-2} s^{-1}] in young (2 weeks old) and old (10-12 weeks old) leaves of two cassava cultivars (M Col 1684 and CM 507-37) with (+) and without (-) fertilizer (F). sd = standard deviation.

Cutivar	F	Young leaves				Old leaves	
		- stress		+ stress		+ stress	
		P_N	sd	P_N	sd	P_N	sd
M Col 1684	+	32.8	3.3	34.5	1.4	6.5	4.9
M Col 1684		30.7	4.0	31.5	3.7	3.3	1.9
CM 507-37	+	37.6	4.5	38.7	5.6	6.7	4.2
CM 507-37	-	35.3	0.5	35.8	2.9	5.5	1.8

Leaf area index (LAI): The cultivar CM 507-37 had higher LAI, with an average of 1.26, compared with 0.99 for M Col 1684 (Fig. 3). Highly significant differences also occurred between the stress (LAI 0.99) and non-stress (LAI 1.25) treatments (LSD = 0.09), and between fertilized (LAI 1.34) and non-fertilized plants (LAI 0.90).

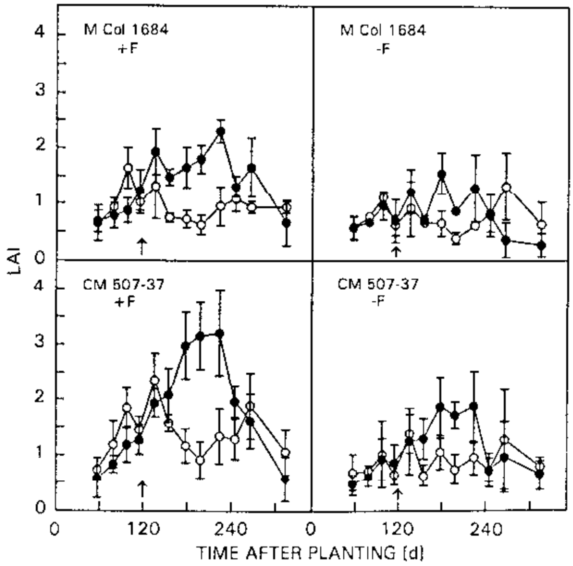

Fig. 3. Leaf area index (LAI) in two cassava cultivars (M Col 1684, CM 507-37) throughout the experiment, with (○) or without (●) stress, with (+F) or without (-F) fertilization. ↑ indicates the initiation of water stress. Bars ± sd.

The seasonal average LAI of cultivar M Col 1684 (nonstressed, fertilized) was 1.36, while under fertilized, stressed conditions, it was 0.96. However, dry root yield at final harvest, 12 months after planting, showed no significant differences between the two treatments. The same trend occurred in cultivar CM 507-37 for the fertilized stress and non-stress treatments.

Hence a greater production of foliage does not imply a greater dry root yield; on the contrary, an excessive leaf development may limit root production. On the other hand, deficient development of leaves has a negative effect on yield (Cock and El-Sharkawy 1988). Reduced leaf area is a defence mechanism by which the cassava plant reacts to water stress.

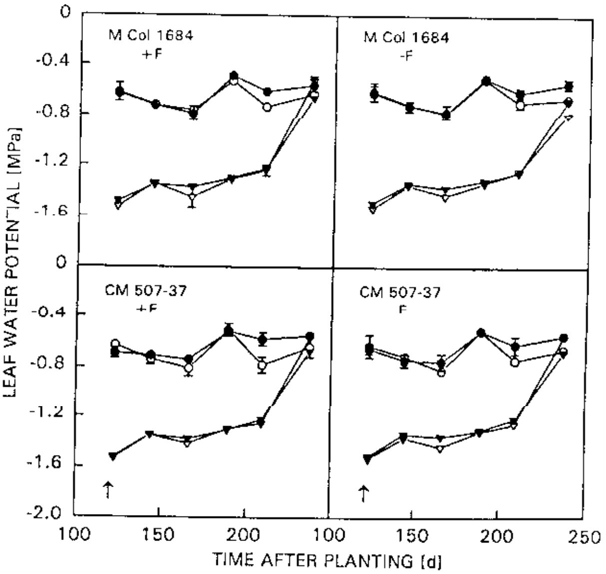

Fig. 4. Leaf water potential of cassava, at 06:00 h with (○) or without (●) stress, or at 12:00 h with (▽) or without (▼) stress, with (+F) or without (-F) fertilization. ↑ indicates the initiation of water stress. Bars ± sd.

Table 3. Seasonal average leaf area index (LAI) and dry root production [kg m^{-2}] at final harvest, 12 months after planting, of two cassava cultivaries with (+) and without (-) water stress (WS), and with (+) and without (-) fertilizer (F). Values within columns followed by the same letter(s) are not significantly different ($p < 0.05$).

Cultivar	WS	F	LAI	Dry root production
M Col 1684	+	+	0.96 cd	0.684 a
M Col 1684	+	-	0.74 d	0.481 bc
M Col 1684	-	+	1.36 b	0.705 a
M Col 1684	-	-	0.89 cd	0.259 d
CM 507-37	+	+	1.37 b	0.614 ab
CM 507-37	+	-	0.90 cd	0.429 bcd
CM 507-37	-	+	1.70 a	0.623 ab
CM 507-37	-	-	1.06 c	0.314 cd

Leaf water potential remained equal, regardless of whether plants were submitted to water stress or not (Fig. 4). An increase in midday leaf water potential was observed in advanced stages of the crop because relative humidity was high (> 75 %) and temperatures were low. The lack of differences in leaf water potential could be partially explained by stomatal closure and the ability of stressed cassava to absorb water from deep soil layers.

Based on these results, we can conclude that cassava tolerates well the prolonged water deficit and has mechanisms that allow it to conserve water, such as stomatal closure, presence of fibrous roots in deeper soil layers, and reduced leaf area to decrease water loss by transpiration (El-Sharkawy *et al.* 1992a, El-Sharkawy 1993). These inherent characteristics of cassava to tolerate prolonged drought underlie the increasing importance of the crop in seasonally dry and semiarid environments (de Tafur *et al.* 1997).

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