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Leaf gas exchange of cassava as affected by quality of planting material and water stress

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Abstract

Field trial was conducted to study the effects of quality of planting material and prolonged water stress on leaf gas exchange of the cassava (*Manihot esculenta* Crantz) cultivar M Col 1684. Nutrient contents of planting material affected rootlet formation, but not leaf gas exchange. Net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were significantly reduced by prolonged water stress. New leaves developed after recovery from water stress showed higher P_N and g_s, as compared to leaves of similar ages of unstressed plants. The higher P_N was associated with higher leaf nutrient contents, indicating that photosynthetic capacity was enhanced in these leaves. These compensating characteristics may partly explain the small yield reduction often observed in stressed cassava.

Additional key words: intercellular CO_2 concentration; *Manihot esculenta*; net photosynthetic rate; nutrient level; stake quality; stomatal conductance; water potential.

Introduction

Where prolonged drought and low-fertility soils are major constraints for the successful production of food crops such as cereals, cassava can produce reasonably well (Cock 1985, El-Sharkawy 1993). In the tropics, most cassava production occurs under erratic rainfall and prolonged dry periods (> 3 months). The plant tolerates prolonged drought by reduction in leaf and top growth at the onset of water stress, partial stomatal closure, and extraction of water from deep soil layers (Connor *et al.* 1981, El-Sharkawy and Cock 1987, El-Sharkawy *et al.* 1992, El-Sharkawy 1993, de Tafur *et al.* 1997a).

The nutrient content of cassava planting material (stakes) significantly affects root yields in the subsequent crops, particularly in poor soils and without fertilizer

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application (Molina and El-Sharkawy 1995). This work evaluates the effects of interaction between stake quality and water stress on leaf gas exchange of the cultivar used by Molina and El-Sharkawy (1995).

Materials and methods

The experiment was carried out in the 1996/1997 season in a drainage field lysimeter (El-Sharkawy and Cock 1987) at the experiment station of the International Centre for Tropical Agriculture in Santander de Quilichao, Cauca Department, Colombia (altitude 990 m; lat. 3°06'N, long. 76°31'W, mean annual temperature 24 °C).

The lysimeter (450 m^2) and its bordering area (12 m wide strip surrounding the lysimeter) were under cassava (2y) and maize (1y) with applications of [g m^{-2} y^{-1}] 5.0 N, 4.3 P, and 8.3 K in the form of a compound fertilizer consisting of 10 : 8.7 : 16.6 of N, P, K. Moreover, the maize crop was incorporated into the soil at tasseling stage before planting cassava. The soil had 5.9 % organic matter; 12 g m^{-3} P (Bray II); 21 Ca, 11 Mg, and 2.5 K me per kg dry soil; with pH of 4.5 and Al saturation of 30 %. Because of these relatively high nutrient contents, cassava was grown without application of fertilizer.

Planting material from the cassava (*Manihot esculenta* Crantz) cv. M Col 1684 was obtained from a 13-year N,P,K trial. Stakes, 20 cm long, were cut 10 months after planting (13th cycle) from the lower woody part of main stems or first branches, and were planted at a density of 1 plant m^{-2} on 21 March 1996. 10 months after planting, contents of nutrients were determined in subsamples of stakes from each mother plant treatment. Another set of stakes was planted in small plastic bags filled with the same soil to evaluate their rooting capacity at an early stage of sprouting.

One half of the lysimeter area and the surrounding border was covered with white plastic at 95 d after planting to initiate water stress that ended on 20 September 1996. The second half of the experimental area received rainfall plus supplementary irrigation on 17 July (30 mm), 24 July (20 mm), and 13 August (20 mm). The total precipitation from March 1996 to January 1997 (2000 mm) was greater than annual pan evaporation (1400 mm), with about 830 mm falling between March and June 1996. Thus excess water was partially stored in the soil profile prior to the initiation of water stress. Four replications for each stake treatments were used within both water regimes. After termination of water stress (86 d of stress), the crop was allowed to recover with rainfall and supplementary irrigation for the rest of the growing season.

Measurements of leaf gas exchange (CO_2 uptake and H_2O loss) were made with an *LI-6200* portable gas analyzer (*Licor*, Lincoln, Nebraska, USA) by enclosing upper canopy leaves in a 4 000 cm^3 chamber for 30 s under a solar radiation higher than 1000 μmol m^{-2} s^{-1} between 08:00-12:00 h. Leaf water potential (Ψ_L) was determined with a *3005* Plant Water Status Console Pressure Chamber (*Soil Moisture Equipment Corp.*, Santa Barbara, CA, USA) using compressed nitrogen. Before leaves were detached, they were enclosed in small plastic bags that contained a small wet towel to minimize water loss from leaves before measurements.

Results and discussion

Effect of soil nutrient status on the nutritional status of stakes and their rooting capacity: Significant differences due to fertilizer application were observed in stakes′ content of N, P, and K but not of Ca and Mg (Table 1). The highest mineral element contents were found in stakes originating from soils fertilized annually with 10 g m^{-2} of N, P, and K. The lack of differences in Ca and Mg contents was probably due to lack of application of a Ca and Mg fertilizer to mother plants. Our findings confirm those of Molina and El-Sharkawy (1995).

Table 1. Nutrient contents of stakes [mg per stake], stake dry mass [g], rootlet length [cm], and dry mass [g] per stake at 50 d after planting in plastic bags. Planting material types are from mother plants that received annually (for 13 years of continuous cassava cultivation) the applications of NPK fertilizers characterized by indexes in g m^{-2}. Averages of four 20-cm long stakes. Values within columns followed by the same letter are not significantly different ($p < 0.05$).

Planting material	Stake dry mass	Rootlet length	Rootlet dry mass	N	P	K	Ca	Mg
$N_0P_0K_0$	12.14 ab	28 ab	0.83 b	85 b	12 b	32 bc	61 a	46 a
$N_5P_5K_5$	13.81 ab	39 a	1.40 ab	103 b	14 b	46 ab	50 a	30 a
$N_{10}P_{10}K_{10}$	16.68 a	40 a	1.88 a	156 a	21 a	65 a	69 a	31 a
$N_{10}P_{10}K_0$	11.34 b	23 b	0.88 b	80 b	14 b	19 c	47 a	33 a

Significant differences due to fertilizer application to mother plants were also observed in stake dry mass and rootlets′ length and mass. Again, the stakes that came from soils fertilized with 10 g m^{-2} each of N, P, and K were the heaviest and had the largest rootlet length and mass (Table 1). Molina and El-Sharkawy (1995) reported that stake sprouting was reduced in the absence of K application to mother plants, irrespective of N and P levels.

Leaf gas exchange: One month after initiation of water stress, significant differences in P_N, g_s, and C_i were found between stress and non-stress treatments (Figs. 1 to 3). The differences were more pronounced in g_s and C_i than in P_N. El-Sharkawy (1993), El-Sharkawy *et al.* (1992), and de Tafur *et al.* (1977a) report similar reductions in P_N and g_s with prolonged mid-season and terminal water stress in several cassava cultivars, including the cv. M Col 1684. The ability of cassava leaves to remain photosynthetically active during prolonged water stress might be partially explained by the absence of a large decrease in the Ψ_L (Fig. 4).

Similar findings were reported by Cock *et al.* (1985), El-Sharkawy *et al.* (1992), and de Tafur *et al.* (1997a). The reasonable stabilization of Ψ_L during prolonged water stress may be attributed to partial stomatal closure (Fig. 2) and to the ability of cassava to extract soil water from deep layers (El-Sharkawy *et al.* 1992, de Tafur *et al.* 1997a).

Stake origin apparently did not significantly affect P_N, g_s, C_i, and Ψ_L (Figs. 1 to 4). Thus the nutritional status of planting material had little or no effect on the photosynthetic performance of leaves and their water status, irrespective of watering regime. Molina and El-Sharkawy (1995) report that leaf canopy, top and storage root biomass are significantly lower in crops originating from stakes that come from unfertilized soils (for eight consecutive years) as compared to those from adequately fertilized soils. Thus factors other than leaf gas exchange, such as higher leaf area

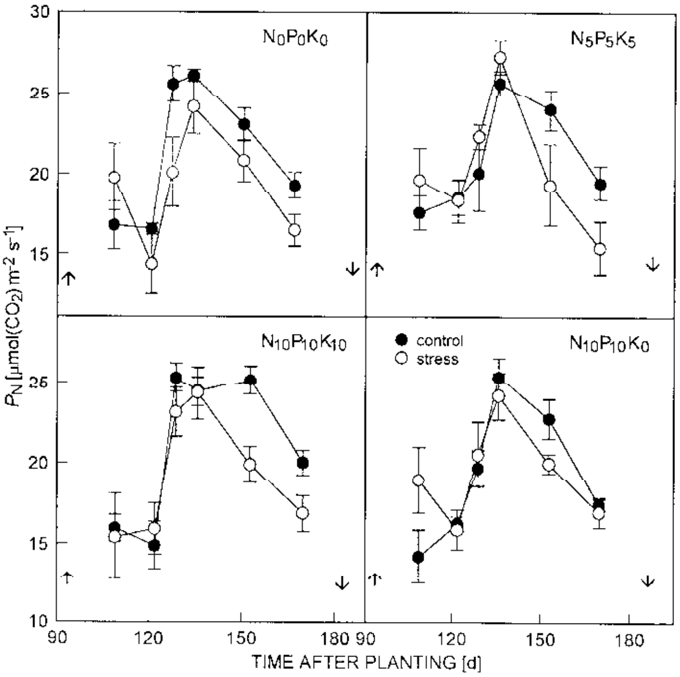

Fig. 1. Effects of stake quality and water stress on net photosynthetic rate, P_N. Plots of mother plants received annually (for 13 years of continuous cassava cultivation) the applications of NPK fertilizers characterized by indexes in g m^{-2}. ↑ = initiation of stress, ↓ = end of stress. Bars = ±SE.

Table 2. Average net photosynthetic rates, P_N [μmol(CO$_2$) m^{-2} s^{-1}], stomatal conductance, g_s [mol m^{-2} s^{-1}], and intercellular CO$_2$ concentration, C_i [μmol mol^{-1}(air)] in variants with (+) or without (-) water stress for new young leaves developed after the water stress termination. For planting material types see Table 1. Values in columns followed by the same letter are not significantly different ($p < 0.05$).

Planting material	Water stress	P_N	g_s	C_i
$N_0P_0K_0$	+	24.4 a	0.73 a	265 a
	-	22.0 bc	0.61 ab	259 a
$N_5P_5K_5$	+	23.9 ab	0.71 a	265 a
	-	21.4 c	0.61 ab	260 a
$N_{10}P_{10}K_{10}$	+	24.5 a	0.71 a	261 a
	-	21.7 c	0.59 ab	256 a
$N_{10}P_{10}K_0$	+	23.8 ab	0.69 ab	259 a
	-	19.3 d	0.56 b	259 a

index and better interception of radiation in crops established from fertilized stakes, might have caused differences in productivity observed by Molina and El-Sharkawy (1995).

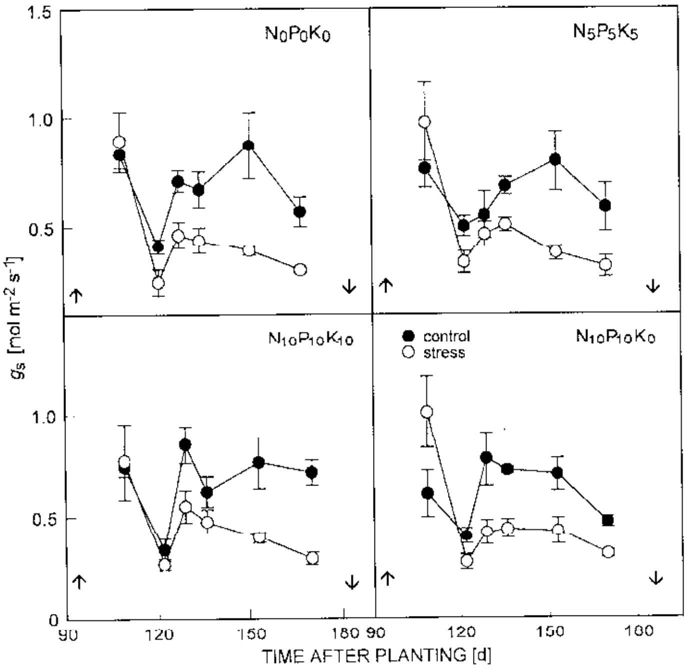

Fig. 2. Effects of stake quality and water stress on stomatal conductance, g_s. For treatments and other explanations see Fig. 1.

Young leaves developed after recovery from stress consistently showed significantly higher P_N and g_s compared with leaves of similar ages in unstressed plants, irrespective of the stake origin (Figs. 5 and 6, Table 2). In contrast, differences in C_i were not significant (Fig. 7, Table 2), indicating that the higher P_N in newly developed leaves after recovery from stress might be due to enhanced CO_2 fixation capacity. This conclusion was further substantiated by the higher nutrient contents, except K, in leaves developed after recovery from stress as compared to leaves from unstressed plants (Table 3). Leaf photosynthesis might be enhanced by greater demands for photoassimilates in the storage roots of previously stressed plants. The consistently lower K contents in leaves developed after recovery from stress, as compared to those in leaves of unstressed plants (Table 3), and the negative correlation between P_N and K content ($r = -0.80$, $p < 0.05$) might indicate that larger volumes of both K and photoassimilates were translocated to storage roots of stressed plants. In cassava, most photosynthates (60 to 70 % of total harvested biomass) are stored in the form of starch in storage roots along with more than 60 % of total absorbed K (El-Sharkawy *et al.* 1992, Pellet and El-Sharkawy 1993, 1994, 1997), thus indicating a close association between the mobilization of both K and photosynthates from the source leaves to the storage root sinks.

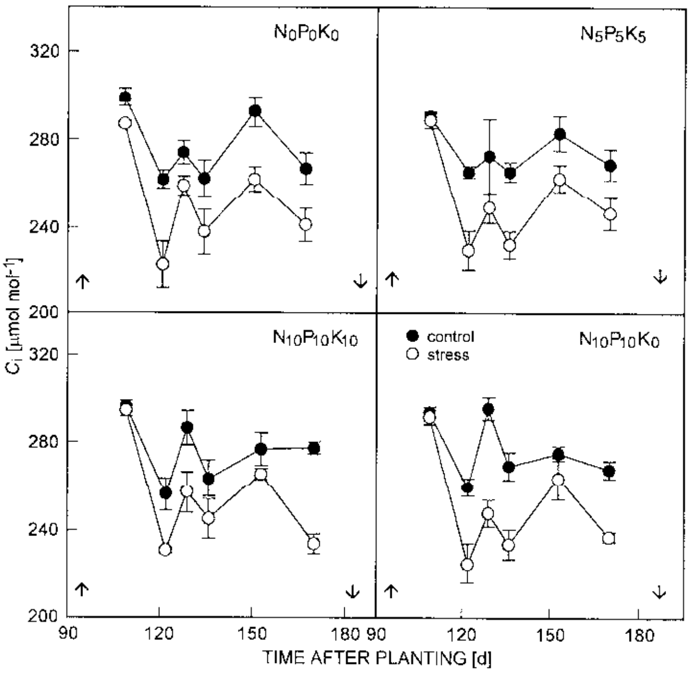

Fig. 3. Effects of stake quality and water stress on intercellular CO_2 concentration, C_i. For treatments and other explanations see Fig. 1.

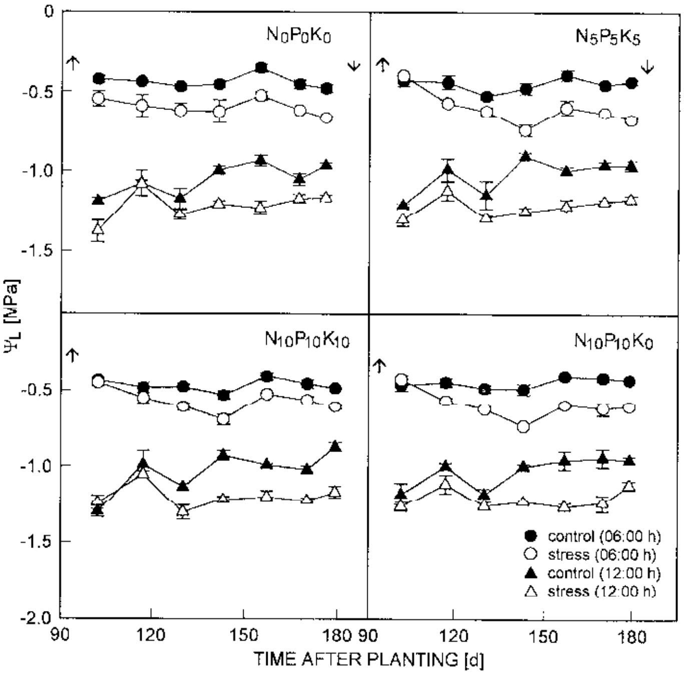

Fig. 4. Effects of stake quality and water stress on predawn (06:00) and midday (12:00) leaf water potential, Ψ_L. For treatments and other explanations see Fig. 1.

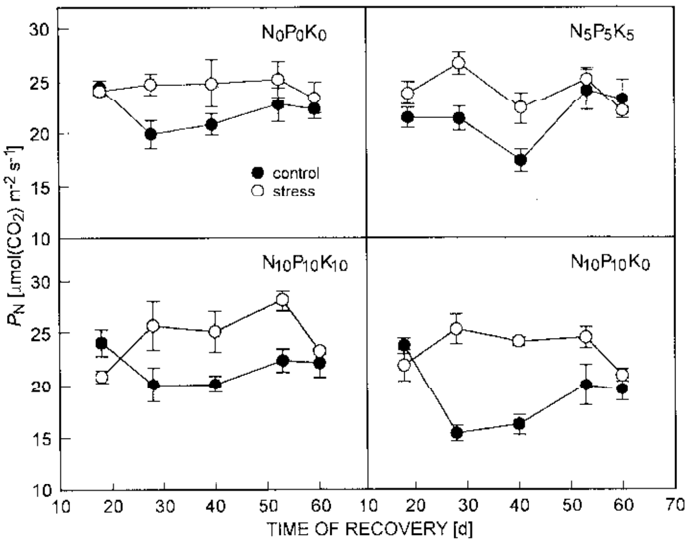

Fig. 5. Effects of stake quality and recovery after water stress on net photosynthetic rate, P_N. For treatments and other explanations see Fig. 1.

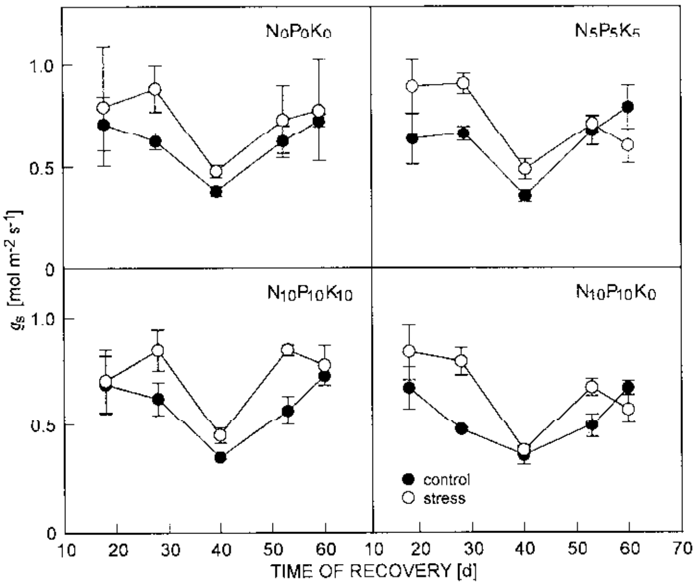

Fig. 6. Effects of stake quality and recovery after water stress on stomatal conductance, g_s. For treatments and other explanations see Fig. 1.

P_N responses to irradiance were similar for both new leaves developed after the recovery from stress and those from unstressed plants, irrespective of the origin of planting material (Fig. 8). In the present trial, the overall averages of dry root yield at 10 months after planting were 0.951 and 0.933 kg m^{-2} for the unstressed and stressed rops, respectively.

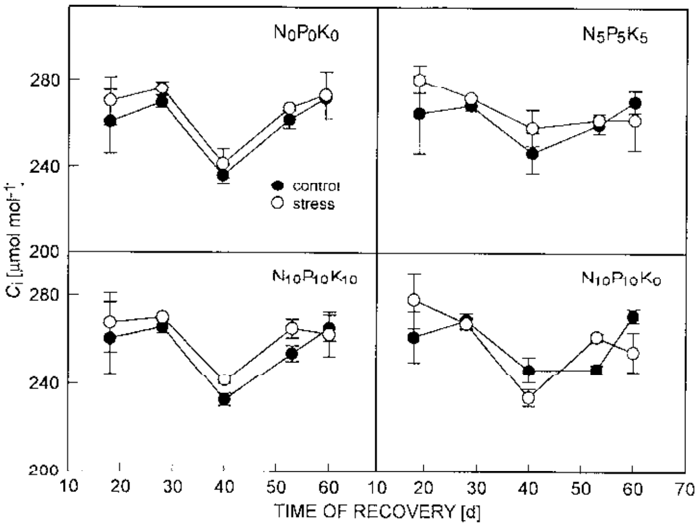

Fig. 7. Effects of stake quality and recovery after water stress on intercellular CO_2 concentration, C_i. For treatments and other explanations see Fig. 1.

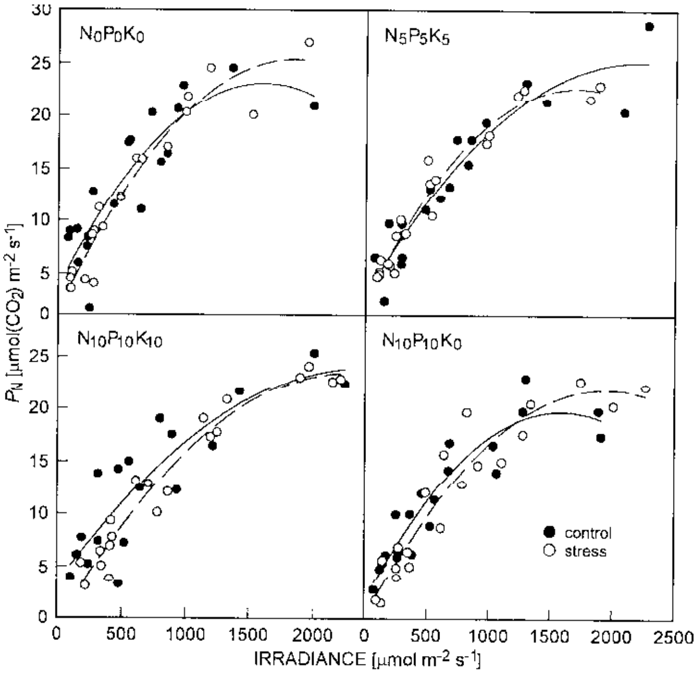

Fig. 8. Responses of net photosynthetic rate, P_N, to irradiance in leaves of well-watered plants (*control*) and young mature leaves formed after the termination of prolonged water stress (*stress*). Each point represents different leaf. Measurements were made 238 d after planting. For treatments and other explanations see Fig. 1.

Table 3. Nutrient concentration [%] after the termination of water stress in variants with (+) or without (-) water stress for young mature leaves developed after the termination of water stress. For planting material types see Table 1. Values are for blended leaf samples (four samples per treatment).

Planting material	Water stress	N	P	K	Ca	Mg
$N_0P_0K_0$	–	4.05	0.27	0.79	1.53	0.41
	-	3.64	0.26	0.99	1.33	0.36
$N_5P_5K_5$	+	4.01	0.27	0.78	1.58	0.41
	-	3.78	0.26	0.95	1.25	0.36
$N_{10}P_{10}K_{10}$	+	3.99	0.26	0.81	1.43	0.42
	-	3.91	0.27	0.96	1.24	0.36
$N_{10}P_{10}K_0$	+	4.09	0.27	0.79	1.37	0.39
	-	3.88	0.24	0.93	1.39	0.38

Based on these results, we conclude that the origin of planting material of cassava and their nutrient contents have little effect on leaf gas exchange characteristics measured under field conditions, irrespective of the watering regime. Although P_N is significantly reduced under prolonged water stress, new leaves developed after recovery from water stress show higher P_N and higher nutrient contents than the leaves of similar ages in unstressed plants. These compensating characteristics may underlie the ability of cassava to produce reasonably well under prolonged water stress (El-Sharkawy 1993), and partly explain why previously stressed cassava plants do not show much reduction in final root yield (El-Sharkawy *et al.* 1992, de Tafur *et al.* 1997a,b).

References

Cock, J.H.: Cassava: New Potential for a Neglected Crop. - Westview, Boulder 1985.

Cock, J.H., Porto, M.C.M., El-Sharkawy, M.A.: Water use efficiency of cassava. III. Influence of air humidity and water stress on gas exchange of field grown cassava. - Crop Sci. **25**: 256-272, 1985.

Connor, D.J., Cock, J.H., Parra, G.E.: Response of cassava to water shortage. I. Growth and yield. - Field Crops Res. **4**: 181-200, 1981.

de Tafur, S.M., El-Sharkawy, M.A., Cadavid, L.F.: Response of cassava (*Manihot esculenta* Crantz) to water stress and fertilization. - Photosynthetica **34**: 233-239, 1997a.

de Tafur, S.M., El-Sharkawy, M.A., Calle, F.: Photosynthesis and yield performance of cassava in seasonally dry and semiarid environments. - Photosynthetica **33**: 249-257, 1997b.

El-Sharkawy, M.A.: Drought-tolerant cassava for Africa, Asia and Latin America. - BioScience **43**: 441-451, 1993.

El-Sharkawy, M.A., Cock, J.H.: Response of cassava to water stress. - Plant Soil **100**: 345-360, 1987.

El-Sharkawy, M.A., Hernández, A. del P., Hershey, C.: Yield stability of cassava during prolonged mid-season water stress. - Exp. Agr. **28**: 165-174, 1992.

Molina, J.L., El-Sharkawy, M.A.: Increasing crop productivity in cassava by fertilizing production of planting material. - Field Crops Res. **44**: 151-157, 1995.

Pellet, D., El-Sharkawy, M.A.: Cassava varietal response to phosphorus fertilization. I. Yield, biomass and gas exchange. - Field Crops Res. **35**: 1-11, 1993.

Pellet, D., El-Sharkawy, M.A.: Sink-source relations in cassava: effects of reciprocal grafting on yield and leaf photosynthesis. - Exp. Agr. **30**: 359-367, 1994.

Pellet, D., El-Sharkawy, M.A.: Cassava varietal response to fertilization: growth dynamics and its implication for cropping sustainability. - Exp. Agr. **33**: in press, 1997.