

# Physiological characteristics of cassava tolerance to prolonged drought in the tropics: Implications for breeding cultivars adapted to seasonally dry and semiarid environments

Mabrouk A. El-Sharkawy

*Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. Present address: A. A. 26360, Cali, Colombia.*

*\*Corresponding author: elsharkawy@telesat.com.co*

Received: 30 September 2007; Accepted: 21 October 2007

The paper summarizes research conducted at International Center for Tropical Agriculture (CIAT) on responses of cassava to extended water shortages in the field aided by modern gas-exchange and water-relation techniques as well as biochemical assays. The aim of the research was to coordinate basic and applied aspects of crop physiology into a breeding strategy with a multidisciplinary approach. Several physiological characteristics/traits and mechanisms underpinning tolerance of cassava to drought were elucidated using a large number of genotypes from the CIAT core germplasm collection grown in various locations representing ecozones where cassava is cultivated. Most notable among these characteristics are the high photosynthetic capacity of cassava leaves in favorable environments and the maintenance of reasonable rates throughout prolonged water deficits, a crucial characteristic for high and sustainable productivity. Cassava possess a tight stomatal control over leaf gas exchange that reduces water losses when plants are subjected to soil water deficits as well as to high atmospheric evaporative demands, thus protecting leaves from severe dehydration. During prolonged water deficits, cassava reduces its canopy by shedding older leaves and forming smaller new leaves leading to less light interception, another adaptive trait to drought. Though root yield is reduced (but much less than the reduction in top growth) under water stress, the crop can recover when water becomes available by rapidly forming new canopy leaves with much higher photosynthetic rates compared to unstressed crops, thus compensating for yield losses with final yields approaching those in well-watered crops. Cassava can extract slowly water from deep soils, a characteristic of paramount importance in seasonally dry and semiarid environments where deeply stored water needs to be tapped. Screening large accessions under seasonally dry and semiarid environments showed that yield is significantly correlated with upper canopy leaf photosynthetic rates, and the association was attributed mainly to nonstomatal (anatomical/biochemical) factors. Parental materials with both high yields and photosynthetic rates were identified for incorporation into breeding and selection programs for cultivars adapted to prolonged drought coupled with high temperatures and dry air, conditions that might be further aggravated by global climate changes in tropical regions.

**Key words:** agriculture, breeding, canopy, carboxylation enzymes,  $C_3$ - $C_4$  intermediate, ecophysiology, growth, leaf photosynthesis, *Manihot* sp., PEP carboxylase, productivity, stomata, water stress, yield

**Características fisiológicas da tolerância da mandioca a secas prolongadas nos trópicos: Implicações para o melhoramento de cultivares adaptadas a ambientes semi-áridos e sazonalmente secos:** Este artigo sumaria resultados de pesquisas conduzidas no Centro Internacional para Agricultura Tropical (CIAT), sobre as respostas da mandioca a períodos prolongados de déficit hídrico, no campo, centrado-se em trocas gasosas, relações hídricas e em ensaios bioquímicos. O objetivo da pesquisa foi coordenar aspectos básicos e aplicados da fisiologia da produção para uma

estratégia de melhoramento utilizando-se de uma abordagem multidisciplinar. Várias características e mecanismos associados com a tolerância da mandioca à seca foram elucidados, usando-se de um grande número de genótipos da coleção do germoplasma do CIAT; os genótipos foram cultivados em várias localidades representantes de ecozonas onde a mandioca é cultivada. Dentre essas características, destacam-se a elevada capacidade fotossintética das folhas da mandioca em ambientes favoráveis e a manutenção de taxas fotossintéticas razoáveis durante períodos prolongados de seca, uma característica crucial para altas e sustentadas produtividades. A mandioca apresenta um controle estomático eficiente sobre as trocas gasosas, a fim de reduzir as perdas de água quando as plantas são sujeitas ao déficit de água no solo ou a altas demandas evaporativas da atmosfera, portanto protegendo as folhas de uma desidratação severa. Durante déficits hídricos prolongados, a mandioca reduz a área de sua copa, via perda das folhas mais velhas e formação de novas e menores folhas, o que reduz a interceptação da luz, outra característica de adaptação à seca. Apesar de a produção de raízes ser deduzida (porém muito menos que a redução do crescimento da parte aérea) sob seca, a cultura pode recuperar-se quando a água se torna disponível, via a rápida formação de novas folhas, com taxas fotossintéticas muito maiores que as de plantas não-estressadas, de modo a compensar pelas perdas de produção; com efeito, a produção aproxima-se da produção de cultivos bem irrigados. A mandioca pode extrair, lentamente, água das camadas profundas do solo, uma característica de grande importância em ambientes semio-áridos sazonalmente secos. A varredura de um grande número de acessos nesses ambientes mostrou que a produção é significativamente correlacionada com as taxas fotossintéticas da parte superior da copa, e essa associação foi atribuída principalmente a fatores não-estomáticos (anatômicos/bioquímicos). Materiais parentais tanto com altos rendimentos e elevadas taxas fotossintéticas foram identificados para incorporação em programas de seleção e de melhoramento de cultivares adaptadas a secas prolongadas associadas com altas temperaturas e ar seco, condições que podem ser ainda mais exacerbadas pelas mudanças climáticas globais nas regiões tropicais.

**Palavras-chave:** agricultura, copa, crescimento, ecofisiologia, enzimas de carboxilação, estômato, estresse hídrico, intermediários  $C_3$ - $C_4$ , melhoramento, PEP carboxilase, produção, produtividade

## INTRODUCTION

The role of physiological research in crop improvement and cropping systems management has recently been reviewed (El-Sharkawy, 2006b). As a branch of basic science, plant physiological research has a fundamental role in advancing the frontier of knowledge that is essential for the better understanding of plants and their interactions with surrounding biophysical environments. It also plays a significant role in supporting other branches of science that deal with the practical application of knowledge and in the development of advanced technologies needed for improving biological systems in general and agricultural productivity in particular. Crop physiology deals with studying cultivated crops with the aim of increasing productivity by enhancing the inherent genetic capacities of crops as well as their adaptability to environments. To be effective in realizing such a goal, physiologists have to work within multidisciplinary research teams committed to a particular crop and/or to multi-cropping systems (El-Sharkawy, 2005).

Furthermore, to be successful, the leader/manager of a multidisciplinary research team should not tolerate potential rivalries between disciplines involved nor the dominance of a particular discipline for research support and funds.

Although research conducted in laboratories and in controlled environments is useful in elucidating a specific plant physiological characteristic or mechanisms underlying certain biological processes and responses to environmental factors affecting growth and productivity, by themselves they are inadequate for creating some benefit to the farmer (Evans et al., 1985; Kramer, 1980, 1981). Field research under representative environments and in relevant cropping systems using a broad genetic base must be conducted not only to verify findings in laboratories and controlled environments but also to generate essential information and insights concerning the real potential of crops under natural conditions as well as their responses to a specific limiting environmental factor (El-Sharkawy et al., 1965; El-Sharkawy, 1993, 2004, 2005, 2006a,b; Long et al., 2006). El-

Sharkawy (2004, 2005, 2006a,b) and Long et al. (2006) have shown that research based only on potted plants grown in greenhouses and in controlled cabinets, without the proper calibration in the field, is a waste of time and resources since in most cases results cannot be extrapolated, or simulated by crop modeling, to describe what may take place in natural environments. Those authors concluded that field research is the only valid ecosystem research in studying plant water relations and crop photosynthesis in relation to productivity. Until recently, the controlled-environment and greenhouse potted-plant scientists (many of whom were members of national science academies) controlled the plant photosynthesis and water relations research and often invoked the misuse of the terminology “adaptation to stress” for “acclimation to stress” to protect their domination over the public-funded scientific establishment and to cover up their failure in contributing to the early discoveries of the  $C_4$  photosynthesis and its implications for plant water use efficiency (El-Sharkawy, 2005, 2006b; El-Sharkawy and Hesketh, 1965, 1986; Begonia and Begonia, 2007). This is not a very good example to teach young people about how science is done nor an efficient way to manage public-funded research. Still, there is a need for good reviews of field work similar to that reported on cassava research done in the tropics (El-Sharkawy et al., 1989; El-Sharkawy and Cock, 1990; El-Sharkawy, 1993, 2004, 2006a,b). Another good example of reviews of field work in the tropics is the one on coffee research recently published in the Brazilian Journal of Plant Physiology by DaMatta and Ramalho (2006).

In view of the ever increasing world human population, particularly in developing countries (Sasson, 1990; Cohen, 1997), increasing demands for food and feed in the coming few decades must be met by enhancing agricultural outputs as well as conserving dwindling natural resources, particularly arable lands and water. In developed and industrial countries of the temperate zone, the gap between the potential productivity of crops and actual yields had been largely closed aided by advanced public and private research that has resulted in improved technologies. On the other hand, in developing countries in general, and in the tropics in particular, agriculture productivity is still far below the potential. This situation will be further aggravated in light of the recognized global

climate changes that might result in adverse effects on agricultural systems and food security in developing countries (Rosenzweig and Parry, 1994; IPCC, 2006, <http://www.grida.no/climate/ipcc/regional/502.htm>). The 2007 Nobel Prize for Peace was jointly awarded to IPCC and the former USA Vice President Al Gore in recognition of their efforts in raising public awareness of the implications of global climate changes for environmental conditions and its consequent adverse effects on agriculture, natural resources and ecosystems in general. With few exceptions, agricultural research in tropical countries has a short history and is inadequately supported by national financial resources due to unfavorable agricultural policies. Furthermore, the benefits from the so-called Green Revolution of the 1960's, supported by international research on major cereal crops, were not equally distributed among continents, countries and crops (Evenson and Gollin, 2003). Moreover, the Green Revolution technologies were based on developing high-yielding new cultivars that required expensive production high-inputs, such as agrochemicals and irrigation facilities that are beyond the reach of the many resource-limited small farmers, particularly in the tropics.

Until three decades ago, crops other than wheat, rice and maize, were not included in the research agenda of the first two commodity-oriented international agriculture research centers, i.e. the International Rice Research Institute (IRRI) in the Philippines and the International Maize and Wheat Improvement Center (CIMMYT, from the Spanish acronym) in Mexico (Wortman, 1981). This situation was largely corrected by the creation of more international research laboratories and centers in Africa, Asia and Latin America dealing with various crops, ecosystems and natural resources management. The International Center for Tropical Agriculture (CIAT, from the Spanish acronym) in Colombia has a world mandate for research on cassava, while the International Institute of Tropical Agriculture (IITA) in Nigeria has a more regional mandate. Research on cassava has received attention and support from many developed countries and from various research/development granting agencies. Before CIAT, with a very few exceptions, cassava was a neglected crop as far as research was concerned in tropical countries where the crop was normally cultivated in marginal lands by resource-limited small farmers and constitutes a main

staple for food and feed for both rural and urban habitants. Physiological information on cassava was, until recently, scarce (Hunt et al., 1977; Cock et al., 1979; Cock, 1985).

The cassava physiology section at CIAT conducted both basic and applied research in coordination with a breeding program and took advantage of the diverse genetic resources available within the extensive cassava germplasm collection as well as the diverse environments within Colombia where cassava is cultivated (El-Sharkawy, 1993; Madeley, 1994). The research covered a wide range of ecophysiological aspects of the crop. Cassava was the first cultivated crop to be considered as a  $C_3$ - $C_4$  intermediate species based on: (i) atypical leaf anatomy including the presence of conspicuous thin-walled bundle-sheath cells with large granal chloroplasts, which are less developed than those in the typical  $C_4$  Kranz leaf anatomy (e.g., El-Sharkawy and Hesketh, 1965, 1986; Laetsch, 1974); (ii) close physical association of chloroplasts with numerous mitochondria and peroxisomes in bundle-sheath and mesophyll cells; (iii) low photorespiration (as determined by  $CO_2$  release from illuminated leaves in a rapid stream of  $CO_2$ -free air, less than 10% of net photosynthesis) and low  $CO_2$  compensation point ( $\Gamma = 20$ - $30 \text{ cm}^3 \text{ m}^{-3}$ ); (iv) ability to recycle all internal respiratory  $CO_2$  within the palisade layer when abaxial stomata of amphistomatous leaves are closed under a wide range of irradiances and temperatures; (v) elevated activities of the  $C_4$  phosphoenolpyruvate carboxylase (PEPC) in leaf extracts (10-30% of activities in maize and sorghum); (vi) high percentage (30-60%) of  $^{14}C$  labeling in  $C_4$  dicarboxylic acids after 5-10 s exposure under illumination; (vii) and immunological analysis and DNA hybridization of PEPC from cassava and wild *Manihot* species against antibodies and *ppc* probes from maize (El-Sharkawy and Cock, 1987a; Cock et al., 1987; Riaño et al., 1987a,b; El-Sharkawy et al., 1989; El-Sharkawy and Cock, 1990; Bernal, 1991; López et al., 1993; Aguilar, 1995; El-Sharkawy, 2004, 2006a; El-Sharkawy and de Tafur, 2007). These characteristics, collectively, underpinned the high photosynthetic rate in normal air ( $P_N > 40 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) in high irradiances ( $> 1800 \mu\text{mol m}^{-2} \text{ s}^{-1}$  of PAR), high leaf temperature from 30 to 40 °C, and in high atmospheric humidities observed in cassava grown in favorable environments (El-Sharkawy et al., 1992a, 1993).

Moreover, leaf photosynthetic rates, as measured in the field, were significantly correlated with both total biomass and root yield of a wide range of cultivars grown across years and environments. The relations were attributed mainly to nonstomatal (biochemical/anatomical) factors (El-Sharkawy, 2004, 2006a). Cassava also tolerates prolonged drought that often exceeded five months aided by partial closure of stomata, deep rooting systems and small leaf canopy. These plant traits make cassava a desirable and adaptable crop, as source for food and feed, in the tropical regions that would be adversely affected by global climate changes (Rosenzweig and Parry, 1994; Kamukondiwa, 1996; El-Sharkawy, 2005; IPCC, 2006).

This paper summarizes some research findings, published and unpublished, on the responses of cassava to extended water shortages in the field where physiological mechanisms and characteristics related to the crop's tolerance to drought were sorted out. Moreover, the research laid the foundations for selection and breeding of improved cultivars adapted to prolonged drought normally encountered in seasonally dry and semiarid environments.

## RESEARCH AT CIAT ON CASSAVA RESPONSES TO EXTENDED WATER SHORTAGES

*Responses to prolonged mid-season water stress:* Research at CIAT (Connor et al., 1981; Porto, 1983; El-Sharkawy and Cock, 1987b) has shown that cassava tolerates a relatively long period of drought once the crop is established. In these studies, using a limited number of varieties, a stress period of 2-3 months was imposed 3-4 months after planting. The crop was later allowed to recover from stress for the rest of the growing cycle with the aid of rainfall and supplementary irrigation.

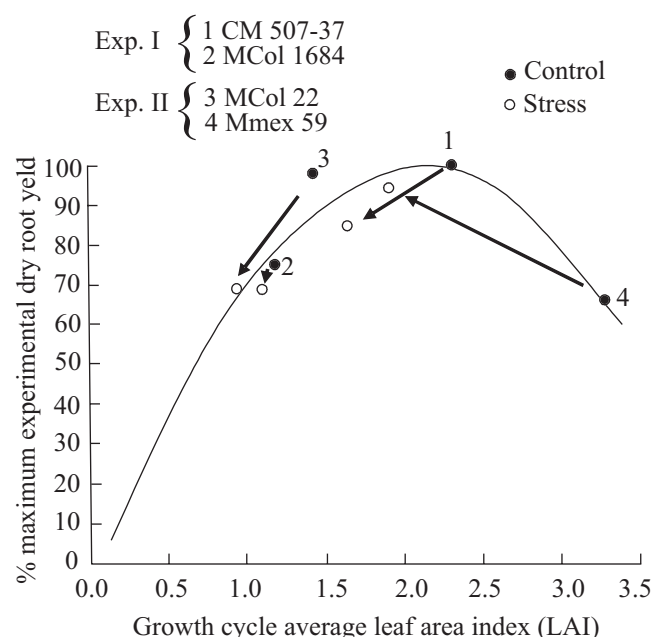
Figure 1 presents the relationship of yield with the seasonal average leaf area index (LAI) for four contrasting varieties, as affected by a prolonged mid-season water stress conducted in two separate field trials (El-Sharkawy and Cock, 1987b). The highest reference (100%) yields were 19 t ha<sup>-1</sup> dry root for CM 507-37 under nonstressed conditions over 345 d in Experiment I (El-Sharkawy and Cock, 1987b) and 11.2 t ha<sup>-1</sup> for M Col 22 under non-stressed conditions for 306 d in Experiment II

(Connor et al., 1981). Compared with the control, the final root yields of the stressed crop were increased in vegetative vigorous varieties (e.g., M Mex 59); were reduced in less vigorous types (e.g., M Col 22); and slightly reduced or remained unchanged in varieties with intermediate vigor (e.g., the parent M Col 1684 and the its hybrid CM 507-37). These responses were closely related to leaf area characteristics (i.e., peak LAI and leaf area duration over the growing cycle), and to patterns of photoassimilate partitioning between top growth (stems and leaves) and storage roots. The vigorous types responded positively to stress because top growth was reduced and the harvest index was increased, whereas the less vigorous types responded negatively because leaf area was drastically reduced to levels below optimal LAI for root yield (El-Sharkawy and Cock, 1987b). The stability of root yields in intermediate types under both favorable and stressful environments stemmed from an ability to maintain leaf area near optimum during a major part of the growing cycle. Also, the relationship between leaf area and storage root yield is very important when cassava is subjected to a cold period coupled with water shortages in the subtropics where leaf area is reduced. Under these conditions, the crop requires a second warm-wet cycle for leaf area recovery and for attaining higher yields (Sagrilo et al., 2006). A similar ideotype approach was followed in studying tolerance to water stress in various crops including winter and spring wheat, maize, sorghum, millets, cowpea and coffee (Kirkham, 1980, 1988; Kirkham et al., 1984; Blum and Sullivan, 1986; Blum and Pnuel, 1990; Bolaños and Edmeades, 1993a,b; Bolaños et al., 1993; Whan et al., 1993; Richards, 2000; Hall, 2004; DaMatta and Ramalho, 2006). This information on the mode of response to water shortages is fundamental for a cassava breeding strategy and points to the need for selecting different plant types for different environments, a strategy later adopted by CIAT and IITA, (Hershey and Jennings, 1992; El-Sharkawy, 1993; Iglesias et al., 1995; Iglesias and Brekelbaum, 1996) and by national cassava programs, as in Brazil (Fukuda et al., 1992-1993).

Nevertheless, CIAT researchers needed to know to what extent cassava can tolerate a more prolonged period of water stress imposed at an earlier stage of growth. They also needed to simulate, as closely as possible, the common cassava-farming practice of planting cassava

near the end of a rainy season, letting it pass through a long period of no rain, and then allowing it to recover in a second wet cycle. This objective was addressed using larger group of varieties.

*Responses to prolonged early water stress:* In the 1987-1988 season, eight cassava varieties (Table 1) were planted in a field drainage lysimeter (the total area, including borders, was about 3000 m<sup>2</sup>) at the CIAT research station at Santander de Quilichao, Cauca Department, Colombia, on 25 November 1987. Planting density was 12 500 plants ha<sup>-1</sup> in ridge, plot size was 25 m<sup>2</sup> and there were four replications per variety and treatment. Plants were adequately fertilized and the plots were kept weed-free manually. Because of rainfall deficits in December 1987 (94 mm) and January 1988 (81 mm), three irrigations were applied to ensure cassava sprouting and establishment. Two months after planting, before imposing the stress, supplementary irrigation was applied to bring the soil-water content to near field capacity within the 2.3-m soil depth. The available soil



**Figure 1.** Dry root yield as a function of growth cycle average leaf area index (LAI) under non-stress and mid-term water stress conditions for four cultivars with different vigor. Data of experiment I for CM 507-37 and M Col 1684 from El-Sharkawy and Cock (1987a); data of experiment II for M Col 22 and M Mex 59 from Connor et al. (1981). Source: El-Sharkawy and Cock (1987b).

water within the 2.3-m profile of the experimental site was about 250 mm (between -0.03 and -1.5 MPa). Half of the experimental area was covered with white plastic sheets to exclude rainfall from day 60 to day 180 after planting. At this stage of growth, cassava had less than 0.8 LAI and less than 2 t ha<sup>-1</sup> total dry biomass, with no visible storage roots (Connor et al., 1981; Porto, 1983; CIAT, 1987-1989; El-Sharkawy and Cock, 1987b; Pellet and El-Sharkawy, 1993, 1997). During the stress period of four months, the control plot received about 540 mm of rain, together with three heavy irrigations within the first and second month, to compensate for the rainfall deficits in that period.

The total amount of water received by the control plot in four months was greater than the potential evapotranspiration at the Quilichao Experiment Station (about 4.2 mm d<sup>-1</sup>). In the stressed plots, water was removed manually immediately after rainfalls and any cracks in the plastic sheets were sealed. The plastic cover was removed during the first week of June 1988. By the end of the stress period, the total water extracted from 2.3 m soil depth ranged among varieties from 168 to 200 mm. From 1 June to 20 October, the total rainfall was 656 mm. Supplementary irrigation to both the stressed and control plots was applied twice in June, July, and August to compensate for the low rainfall during that period. The total rainfall received from planting to harvest was 1406 mm in the control and 865 mm in the stressed plots.

During the stress period, field measurements of leaf gas exchange, both CO<sub>2</sub> uptake and H<sub>2</sub>O loss, were made with a portable, infrared CO<sub>2</sub> analyzer (LI-COR model LI-6000) on single, attached, upper canopy leaves at solar radiation greater than 1000 μmol m<sup>-2</sup> s<sup>-1</sup> of PAR. These measurements were normally made between 0900 and 1300 h once a week within the first two months, and once every two weeks within the last two months of stress. Light interception, leaf water potential, and soil water content were also monitored. Final harvest was made on 20 October 1988 (11 months after planting) and the total standing biomass, root yield and dry matter contents of roots were determined.

Table 1 summarizes data of final standing total biomass, root yields, harvest index, and dry matter contents of storage roots. In the control plot, the total dried biomass ranged (in round figures) among varieties

from 23 to 38 t ha<sup>-1</sup>, fresh roots from 42 to 60 t ha<sup>-1</sup>, dried roots from 14 to 21 t ha<sup>-1</sup>; dry matter contents from 32% to 39%; and the harvest index from 45% to 71%. In the stressed plot, the ranges were (again in round figures) 18 to 28 t ha<sup>-1</sup> for total biomass, 41 to 59 t ha<sup>-1</sup> for fresh roots, 14 to 19 t ha<sup>-1</sup> for dried roots, 30% to 38% for dry matter contents, and 62% to 76% for harvest index.

There were notable varietal differences in response to stress. Fresh and dried-root yields were decreased by stress in the parent M Col 1684, whereas they increased in its hybrid CM 507-37. Previous studies with these two genetically related varieties (CM 507-37 is a hybrid between M Col 1684 and M Col 1438) have shown that CM 507-37 is more vegetative vigorous and leafy (El-Sharkawy and Cock, 1987b, El-Sharkawy et al., 1992b). In other varieties, the yields were relatively unchanged, except for CM 2136-2, where dried-root yields decreased notably, mainly because of reduction in dry-matter contents from 35.5% to 31.1%.

Compared with the control, water stress across all varieties caused a reduction in total biomass by 12%, no change in fresh root yields, a reduction in dried-root yields by 3.4%, a reduction in dry matter contents by 3.3%, and an increase in the harvest index by 10%. These data clearly demonstrate cassava's ability to tolerate prolonged water stress when it is induced gradually at an early stage of growth. Furthermore, the crop is able to recover and compensate, in terms of economic yields, from the adverse effects of stress. In areas with intermittent rainfall and with long periods of drought, cassava should produce reasonably well, providing good crop management (e.g., weed control and adequate fertilization) is practiced and cassava is grown in deep soils with good water-holding capacity.

The physiological mechanisms that underlie cassava's tolerance of severe water stress are illustrated by data in Tables 2 and 3 and Figures 2, 3 and 4. The capacity of cassava leaves to fix atmospheric CO<sub>2</sub>, a basic process for dry matter accumulation, during the stress period was 80% of that in the control (Table 2, Figure 2). This indicated that the photosynthetic process in cassava is not greatly inhibited by prolonged stress, an advantage that many other field crops do not have.

A second and important physiological mechanism of cassava leaves is their ability to partly close their stomata

**Table 1.** Final yields and biomass of eight cassava varieties as affected by an early and prolonged period of water stress. From day 60 to 180 after planting, plants were deprived of rainfall and then were allowed to recover under irrigation and rainfall for the rest of the growth cycle. Rainfall was excluded by covering the soil of the stresses plot with plastic sheets. The experiment was conducted at Santander de Quilichao, Cauca, Colombia; the planting date was 25 November 1987, and the cassava was harvested on 20 October 1988. Source: CIAT (1987-1989).

Variety	Control					Stress				
	Dry biomass	Fresh yield	Dry yield	Dry matter in roots	Harvest index	Dry biomass	Fresh yield	Dry yield	Dry matter in roots	Harvest index
	t/ha			%		t/ha			%	
M Col 1684	27.0	50.5	16.9	33.5	63	18.2	41.8	13.9	33.1	76
CM 489-1	26.4	59.6	18.8	31.6	71	26.8	59.0	17.5	29.6	65
CM 507-37	22.6	42.2	14.1	33.3	62	24.0	52.6	17.2	32.6	72
CM 523-7	25.8	42.7	16.3	38.2	63	26.9	45.6	17.4	38.2	65
CM 922-2	24.8	42.7	16.9	39.4	68	26.0	44.3	17.0	38.3	65
CM 1335-4	29.8	51.6	20.2	39.3	68	26.5	51.0	19.1	37.5	72
CM 2136-2	38.0	58.7	20.9	35.5	55	27.7	55.4	17.3	31.1	62
CM 3306-32	33.8	41.3	15.2	36.7	45	24.5	41.1	15.2	37.0	62
Average	28.5	48.7	17.4	35.9	61	25.1	48.9	16.8	34.7	67
Difference due to stress (%)						<b>-12</b>	<b>0.0</b>	<b>-3.4</b>	<b>-3.3</b>	<b>+10</b>
LSD ( $P=0.05$ )	3.1	4.5	2.0	3.9	5	2.3	4.1	1.8	3.7	6

**Note:** The small reduction in dry root yield was due mainly to reduction in dry matter contents of roots. The larger reduction in total biomass was attributed to a larger reduction in shoot biomass, compared to reduction in storage roots, and hence, a higher harvest index under stress.

in response to water stress. For example, in the experiment, there was an average 43% reduction in leaf conductance to water vapor in stressed plots (Table 2) and consistent reduction over the stress period, compared to the control (Figure 3). The partial closure of stomata enabled cassava leaves to maintain, to some extent, the midday leaf water potential at levels comparable with those of cassava leaves in the control plot. Leaf water potentials at 1400 h across all varieties were -1.13 and -1.12 MPa for the control and stressed leaves, respectively (Table 3). This is another comparative advantage for cassava in dry areas, compared to other crops with poorer stomatal control.

In addition to its beneficial effect by preventing severe leaf dehydration, and consequently preventing impairment to photosynthetic capacity of the leaf, the partial closure of stomata reduces water loss through transpiration (Figure 4), thereby maximizing water-use efficiency, WUE (i.e., the amount of  $\text{CO}_2$  fixed per amount of water transpired). Across all varieties, there was 39% increase in intrinsic leaf water use efficiency ( $P_N/g_s$ ) in stressed crops over the control (Table 2).

A third and equally important physiological mechanism that enables cassava to withstand severe water stress is its ability to maintain a predawn leaf water potential comparable with that of unstressed cassava. In the experiment, leaf water potentials at 0600 h across all varieties were -0.39 and -0.40 MPa for the control and stressed plants, respectively (Table 3). This was partly achieved by reducing total leaf area (as indicated by the 31% reduction in light interception in the stressed plot, Table 2), thereby reducing total canopy transpiration, and by slow withdrawal of water from the deeper layers of the soil profile (Figure 5) (Connor et al., 1981; Porto, 1983; CIAT, 1987-1989; El-Sharkawy and Cock, 1987b; El-Sharkawy et al., 1992b; de Tafur et al., 1997a; Cadavid et al., 1998; El-Sharkawy, 2006a). During water stress, cassava fine roots extend for more than 2 m into deeper, wetter soil from where cassava can extract between 20% and 40% of its total water uptake (CIAT, 1987-1989; El-Sharkawy et al., 1992b). This is of paramount importance in areas with bimodal rainfall patterns and those with one short-wet annual period where excess water percolates deeper in soil profile and, hence, it could be extracted

**Table 2.** Leaf photosynthetic rate ( $P_N$ ) ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), stomatal conductance to water vapor diffusion ( $g_s$ ) ( $\text{mmol m}^{-2} \text{ s}^{-1}$ ), mesophyll conductance to  $\text{CO}_2$  diffusion ( $g_m$ ) ( $\text{mmol m}^{-2} \text{ s}^{-1}$ ), and irradiance interception (I) (%) as affected by an early and prolonged period of water stress.  $P_N/g_s$  ( $\mu\text{mol mmol}^{-1}$ ) indicates the average leaf intrinsic water-use efficiency. Values are means of all measurements made during the stress period from day 60 to day 180 after planting. Measurements were made weekly for the first two months and every two weeks in the last two months of stress (12 measurements x three replications). Source: CIAT (1987-1989).

Variety	Control				Stress			
	$P_N$	$g_s$	$g_m$	I	$P_N$	$g_s$	$g_m$	I
M Col 1684	21.4	815	85	64	18.0	485	76	46
CM 489-1	25.6	1001	104	58	19.6	557	89	37
CM 507-37	23.1	940	92	62	17.3	515	72	45
CM 523-7	24.1	937	97	68	16.2	440	69	42
CM 922-2	25.8	992	102	58	22.3	553	99	37
CM 1335-4	20.6	833	82	61	18.2	565	77	50
CM 2136-2	26.2	1033	104	65	20.6	606	86	37
CM 3306-32	24.9	850	101	63	17.8	492	78	51
LSD ( $P = 0.05$ )	2.1	97	11	NS	1.8	67	9	6
Average of all varieties	<b>24</b>	<b>925</b>	<b>96</b>	<b>62</b>	<b>19</b>	<b>527</b>	<b>81</b>	<b>43</b>
Difference due to stress(%)					<b>-21</b>	<b>-43</b>	<b>-16</b>	<b>-31</b>
$P_N/g_s$		<b>0.026</b>				<b>0.036</b>		

NS = non-significant,  $P > 0.05$

**Note:** The larger reduction in  $g_s$  than in  $P_N$  under stress resulted in *ca.* 39% increase in leaf intrinsic water use efficiency. The reduction in irradiance interception under stress was attributed mainly to smaller leaf canopy (*i.e.* lower LAI). Under stress small-sized new leaves are formed at a slower rate, compared to unstressed crop. Since under stress harvest index increases (see Table 1), reduction in irradiance interception will lead to less crop transpiration rate, and hence, to greater crop water-use efficiency in terms of storage root production. Moreover, when stressed plants recover in wet conditions, they rapidly form new leaf canopy with even higher leaf photosynthetic rates than those in unstressed leaves, thus final yield approaches values obtained in well-watered plants (see Tables 1, 4; El-Sharkawy and Cock, 1987b; El-Sharkawy et al., 1992b, 1998; El-Sharkawy, 1993, 2006a; Cayón et al., 1997; El-Sharkawy and Cadavid, 2002). Under prolonged drought (> 5 months) in semiarid environments with less than 500 mm of effective annual rainfall, cassava survives and produces reasonable yields (3 to 5 t DM ha<sup>-1</sup> with improved cultivars) which can be greatly increased (2-3 times) with a second cycle of rainfall (see Tables 6 and 7).

during long dry periods.

Also, it is possible that the phenomenon of “hydraulic lift” [*i.e.*, nocturnal uptake of water from deeper wet soil layers that is transported and then released from fine roots into dryer top soil layers; see, for example, Mooney et al. (1980), Richards and Caldwell (1987), Caldwell and Richards (1989), Dawson (1993), Squeo et al. (1999)] occurs in cassava since predawn water potential in water-stressed plants always remained as high as in well-watered plants. This might be the case because the majority of fine roots exist in the top 0.40 m and a fewer portion of roots penetrate deeper layers (Connor et al., 1981; El-Sharkawy and Cock, 1987b) where a substantial water extraction occurs (Figure 5). Water uptake from upper layer (0.40 m) continued during long period of water stress with decreasing patterns over time (Figure 5;

El-Sharkawy et al., 1992b, de Tafur et al., 1997a, El-Sharkawy, 2006a), thus indicating the existence of available water in this layer. Another characteristic that might be implicated in cassava tolerance to prolonged water stress is the obligate association with vesicular-arbuscular mycorrhizal fungi (VAM) (Howeler and Sieverding, 1983; Sieverding and Howeler, 1985). Among 20 cassava cultivars growing in large pots outdoors, the percent infected root length under stress varied from ~50 to ~90%, and these values were highly correlated with total plant root length across cultivars ( $r = 0.955$ ,  $P < 0.001$ ) (Sieverding et al., 1985). There is some evidence that plant-VAM associations may confer tolerance to water stress, particularly in species with low fine root density (Hayman, 1980; Nelsen and Safir, 1982; Ellis et al., 1985; Safir, 1985; Augé et al., 1987; Khalvati et al., 2005).



**Table 3.** Leaf water potential (-MPa) of eight cassava varieties measured from 0600 to 1400h as affected by an early and prolonged period of water stress. Values are means of all measurements made during the stress period from day 60 to day 180 after planting. Measurements were made with the pressure chamber technique weekly for the first two months and every two weeks in the last two months of stress (12 measurements x three replications). Source: CIAT (1987-1989).

Variety	Control plants				Stressed plants			
	0600 h	0800 h	1100 h	1400 h	0600 h	0800 h	1100 h	1400 h
M Col 1684	0.38	0.69	0.99	1.07	0.40	0.80	1.02	1.07
CM 489-1	0.38	0.76	1.05	1.10	0.41	0.83	1.09	1.15
CM 507-37	0.38	0.79	1.08	1.19	0.39	0.88	1.16	1.18
CM 523-7	0.40	0.77	1.04	1.09	0.39	0.83	1.06	1.09
CM 922-2	0.39	0.75	0.98	1.11	0.42	0.87	1.05	1.12
CM 1335-4	0.38	0.80	1.12	1.20	0.38	0.87	1.19	1.19
CM 2136-2	0.38	0.80	1.12	1.18	0.43	0.94	1.19	1.15
CM 3306-32	0.42	0.72	1.02	1.09	0.41	0.76	0.97	1.02
Average of all varieties	<b>0.39</b>	<b>0.76</b>	<b>1.05</b>	<b>1.13</b>	<b>0.40</b>	<b>0.85</b>	<b>1.09</b>	<b>1.12</b>

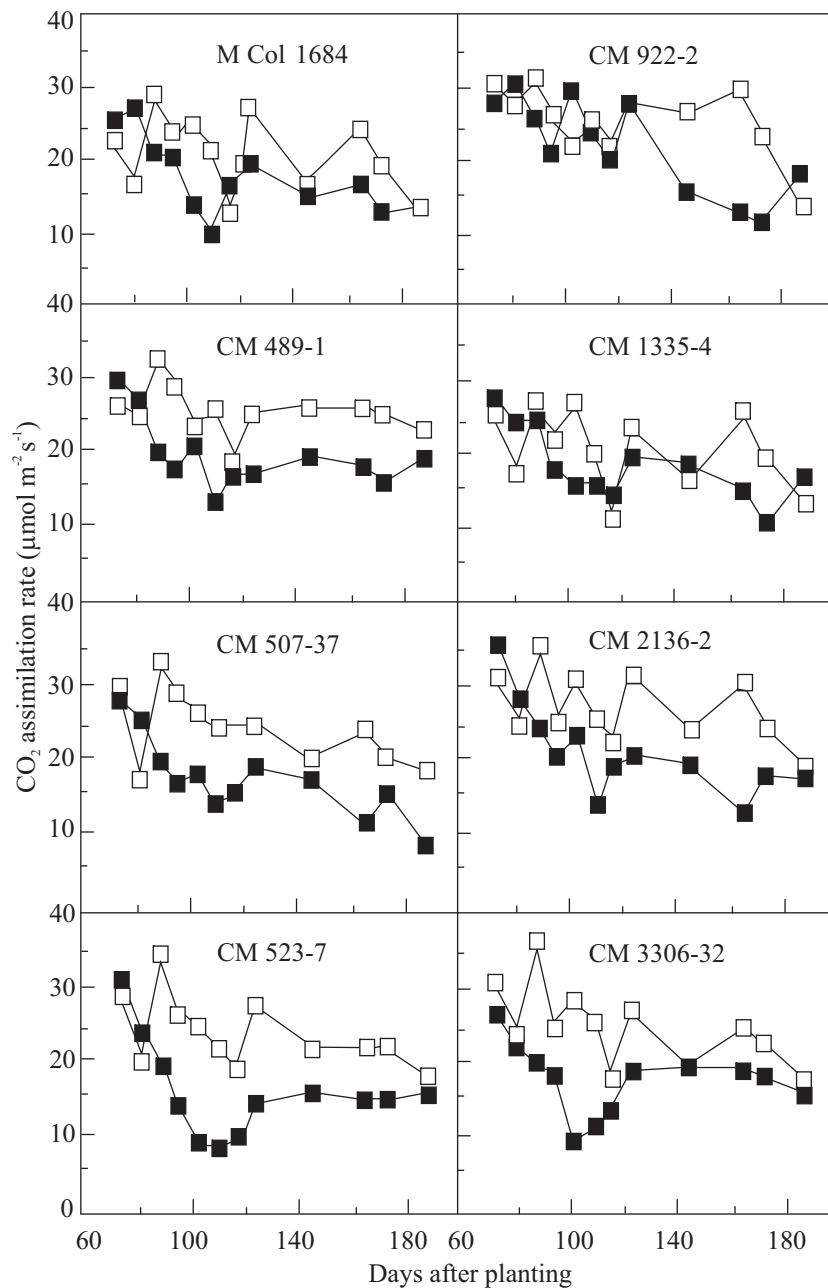
**Note:** The lack of large changes in leaf water potential during the day between unstressed and stressed crops. Average predawn (as measured at 0600 h) and midday (as measured at 1400 h) water potential values were not significantly different between the two watering regimes, indicating the tight stomatal control over water losses. The partial closure of stomata under stress (see Table 2 and Figure 3) reduced leaf transpiration rate (see Figure 4), and, hence, led to stable leaf water content. This stomatal mechanism is beneficial in preventing severe leaf dehydration and impairment of the photosynthetic process as indicated by the  $P_N$  values under stress being *ca.* 80% those in unstressed leaves (see Table 2). Cassava tolerates prolonged water shortages via *stress avoidance mechanism*. When stomatal closure is coupled with rooting system that penetrates into deep wet soil layers (see Figure 5 for patterns of water extraction), crop water use efficiency is maximized under drought conditions. These characteristics are beneficial in ecosystems where excess rainfall is partially stored in deeper soil layers.

Compared to cereal crops, cassava has a sparse fine root system and the extensive fungal hyphae-network in the soil may increase water absorption capacity of infected roots. By using a new split-root hyphae system in barley plants under well-watered and water-stressed conditions in growth chamber, Khalvati et al. (2005) found that water was transported from the fungi hyphae to barley root compartment under water stress, as compared to non-hyphae treatment. VAM-infected plants suffered less (relative to non-infected plants) from water stress in terms of leaf elongation rate, leaf turgor pressure, stomatal conductance and photosynthetic rate. These parameters indicate a better plant water status in VAM-infected plants.

A fourth mechanism underlying tolerance to drought is the ability of cassava to compensate partly for previous losses in dry matter production, due to water stress, by an increase in leaf canopy area (El-Sharkawy and Cock, 1987b; El-Sharkawy et al., 1992b) and by higher photosynthetic rates in the newly developed leaves after recovery, as compared to the unstressed plants (Figure 6) (El-Sharkawy, 1993, Cayón et al., 1997; de Tafur et al., 1997a; El-Sharkawy, 2006a). These higher photosynthetic rates in new leaves of previously stressed cassava were

associated with higher leaf conductances, higher nutrient contents, as well as with stronger sinks for carbohydrate in storage roots (Cayón et al., 1997).

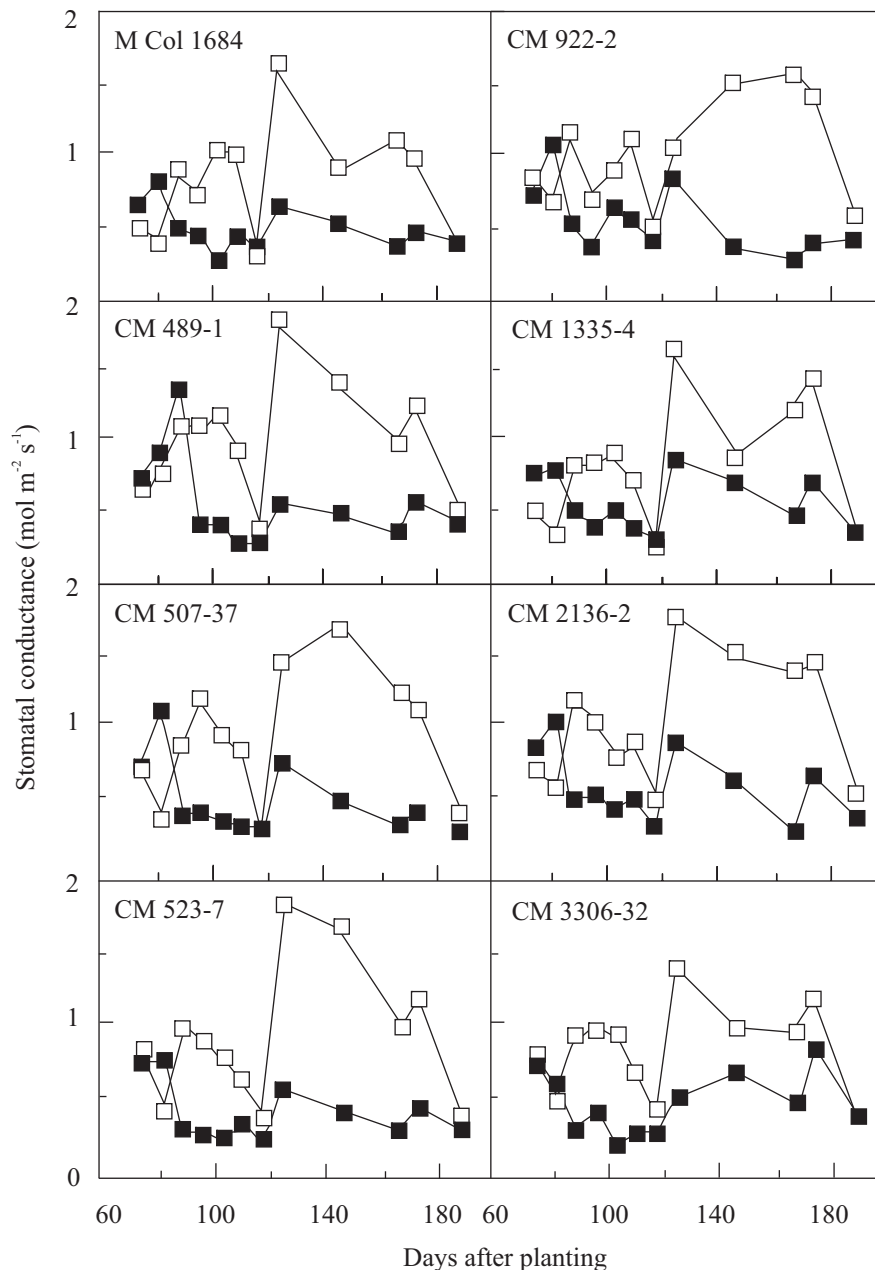
Not only can cassava tolerate long periods of soil water deficits aided with the above-mentioned inherent mechanisms, but it can also react to changes in atmospheric humidity (Figure 7) (Connor and Palta, 1981; El-Sharkawy and Cock, 1984, 1986, 1990; El-Sharkawy et al., 1984, 1985, 1989; Cock et al., 1985; Berg et al., 1986; El-Sharkawy, 1990, 1993, 2004, 2006a; Oguntunde, 2005, Oguntunde and Alatise, 2007). Cassava leaf stomata are sensitive to air humidity, irrespective of soil water content; they close rapidly in dry air when evaporation is high under field conditions, which may be translated into high leaf water potential. This mechanism enables cassava to maximize its WUE during periods of prolonged drought. When air humidity is high (e.g., early in the morning and during rainy periods), the stomata remain open. Thus, in a humid atmosphere and in the presence of soil water deficits, cassava leaves remain photosynthetically active and the crop can produce well; for example, in the Pacific coast of Ecuador, cassava produces 8 to 12 t ha<sup>-1</sup> of fresh roots with only 400 mm of rainfall in 3-4 months. In that region, the intensity of solar



**Figure 2.** Response of cassava leaf photosynthesis to prolonged water stress (120 days), imposed at 60 days after planting. (□ Control; ■ stress.) Source: CIAT 1987-1989 report.

radiation is low because of cloudy skies and, hence, evaporation is low. A similar situation occurs in the Pacific coast of Peru where rainfall is very low but there is an intense fine mist that persists for hours, allowing stomata to remain partly open and the leaf to actively fix CO<sub>2</sub> at a lower rate of transpiration. Thus, WUE at the leaf level (CO<sub>2</sub> uptake per H<sub>2</sub>O loss) and at the crop level for

the whole growing cycle (dry matter produced per total water loss) are maximized in this case. Cock et al. (1985) found that increasing air humidity by fine misting from 1000 h to 1500 h, in a large cassava field experimental plot that was kept wet via irrigation and protected from wind drift by hedge rows of tall elephant grass at the CIAT Experiment Station, Palmira, Valle Department, Colombia,

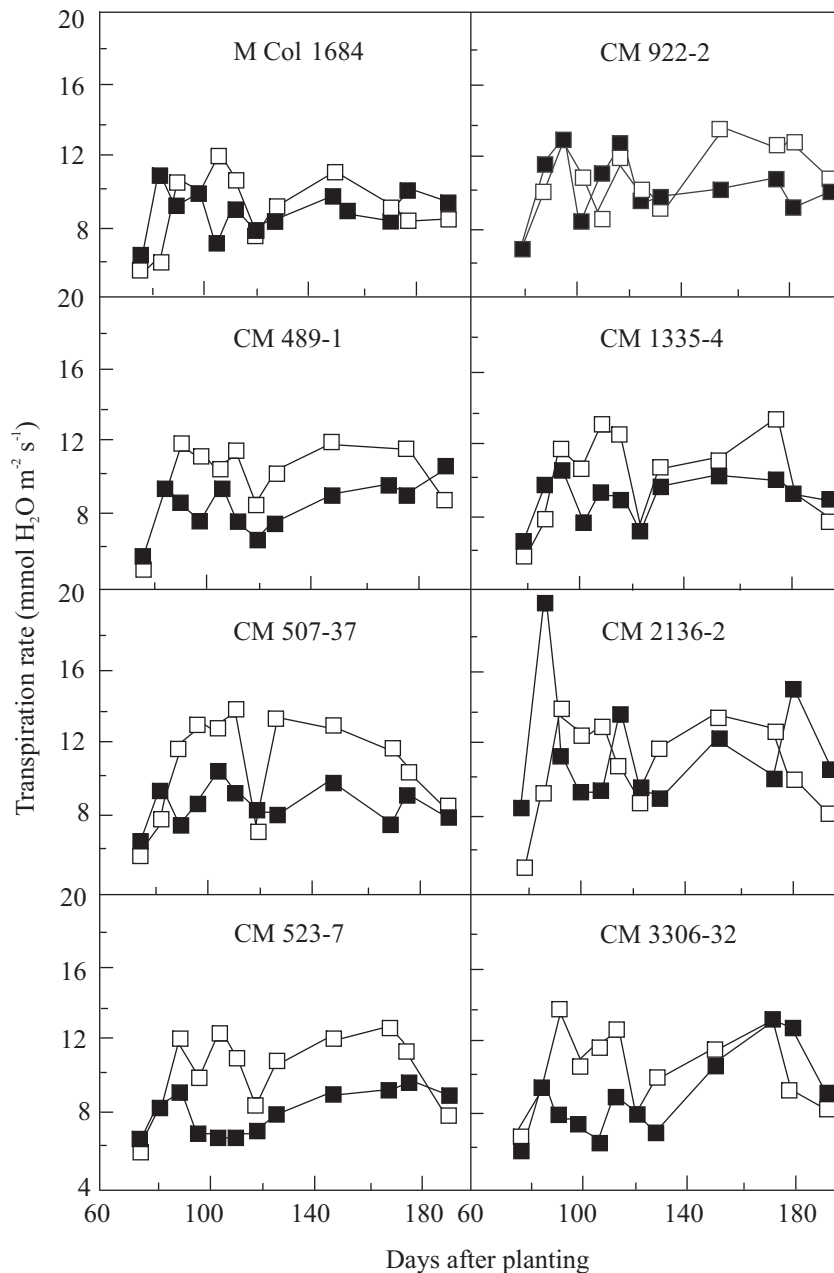


**Figure 3.** Response of cassava stomata to prolonged water stress (120 days), imposed at 60 days after planting. (□ control; ■ stress).

resulted in both higher leaf photosynthesis and higher root yields than in the adjacent unmisted plot that was equally irrigated. Moreover, leaf photosynthetic rate was significantly and positively correlated with air humidity, indicating stomatal reactions to air humidity even in a wet soil (Figure 8).

Coupled with stomatal sensitivity to air humidity is the strong leaf heliotropic response that allows leaves to

track solar radiation early in the morning and late afternoon when the leaf-to-air water vapor deficit (VPD) is low. At midday when solar elevation is high and VPD is greatest, cassava leaves bend downward (i.e., leaf drooping movement) irrespective of soil water content and leaf turgor pressure (El-Sharkawy and Cock, 1984; Berg et al., 1986). The net result of these two leaf movements is to maximize light interception and total

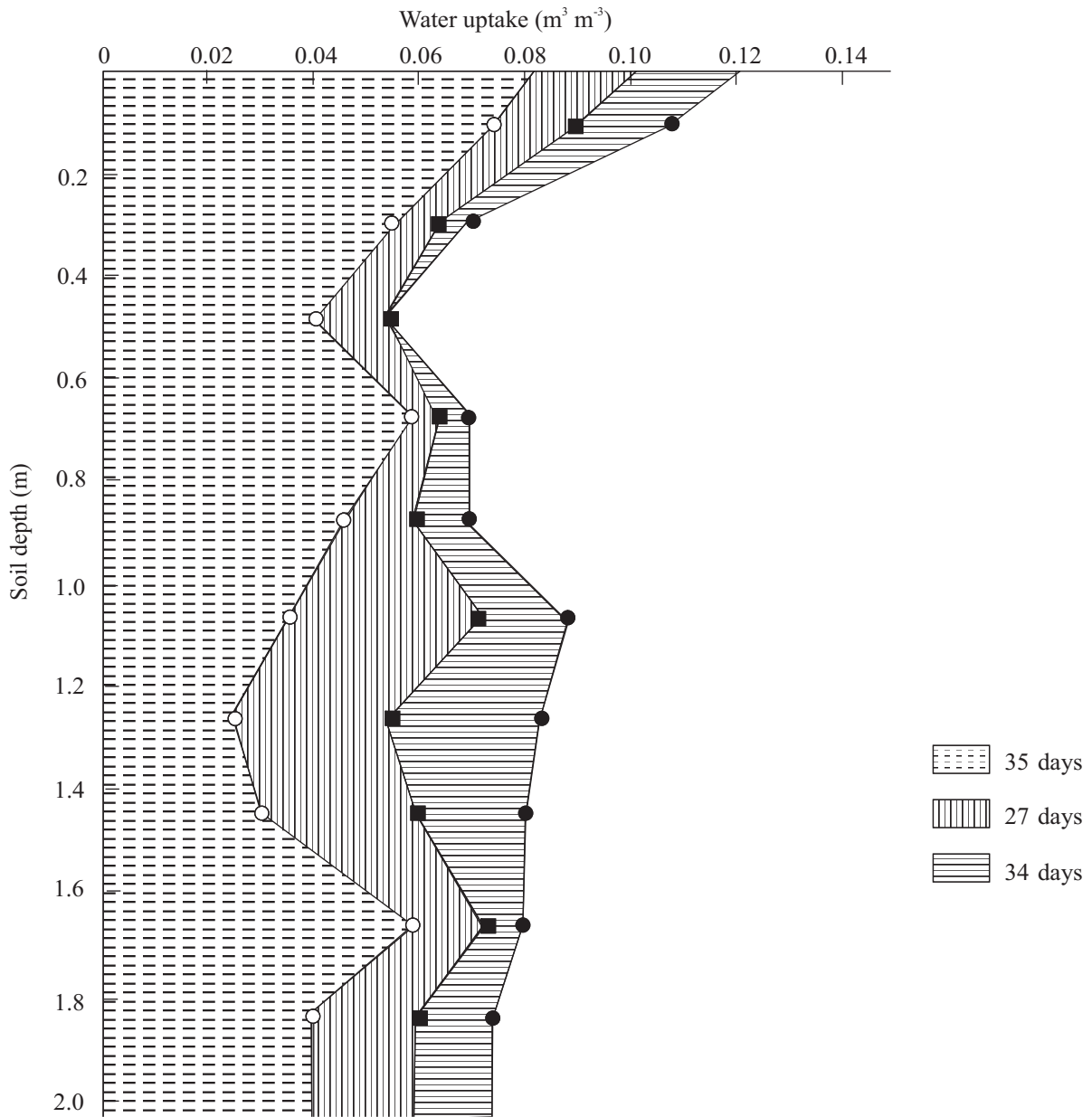


**Figure 4.** Response of cassava leaf transpiration to prolonged water stress (120 days), imposed at 60 days after planting. (□ control; ■ stress). Source: CIAT (1987-1989) report.

canopy photosynthesis when WUE is greatest, and to minimize light interception when WUE is least.

In the present trial, the four months during which soil water stress was imposed coincided with a rainfall peak (total rainfall in April and May 1988 at Quilichao was 400 mm). During April and May 1988, the last two months of the stress period, the photosynthetic rates of the

stressed plants were 60% to 70% of those in the control plants (Figure 2). This remarkable photosynthetic activity of the stressed cassava can be attributed partly to the favorable effects of high humidity which kept the stomata partly open (Figure 3). It may be concluded that cassava is extremely tolerant (or resistant) to prolonged drought because of multiple-inherent morphological,

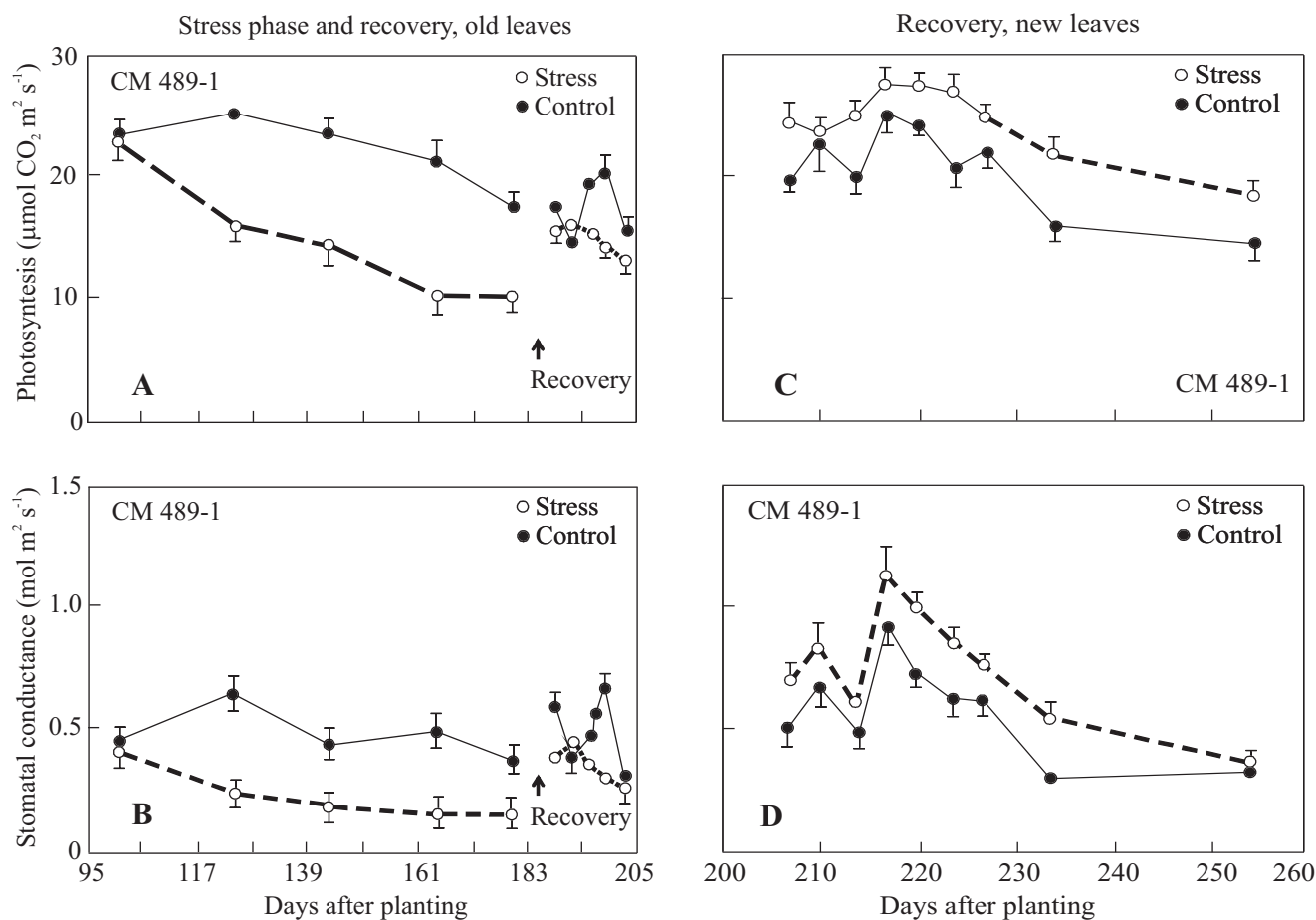


**Figure 5.** Water uptake of M Col 1684 from different layers of soil at Quilichao, Colombia, as a function of time after excluding rainfall (the soil was irrigated to field capacity before being covered with white plastic sheets from 22 September 1986 to 5 January 1987). Data average of four profiles. Source: CIAT (1987-1989) report.

structural and physiological plant traits that allow the crop to obviate the negative effects of severe water stress.

The same trends in responses to extended water deficits imposed at early (2-6 months after planting), mid-season (4-8 months after planting) and terminal (6-12 months after planting) growth stages were observed in a 3-yr field trial with four contrasting cultivars that differed

in their vigor (CIAT, 1992, 1993; Caicedo, 1993; El-Sharkawy et al., 1998; El-Sharkawy and Cadavid, 2002; El-Sharkawy, 2006a). Across cultivars there were no significant differences in root yield among water regimes, but there were significant differences among cultivars indicating genotypic x treatment interactions ( $P < 0.01$ ) (Table 4). Similar responses were observed in the Sudan Savanna zone of Nigeria using variation in the soil-water

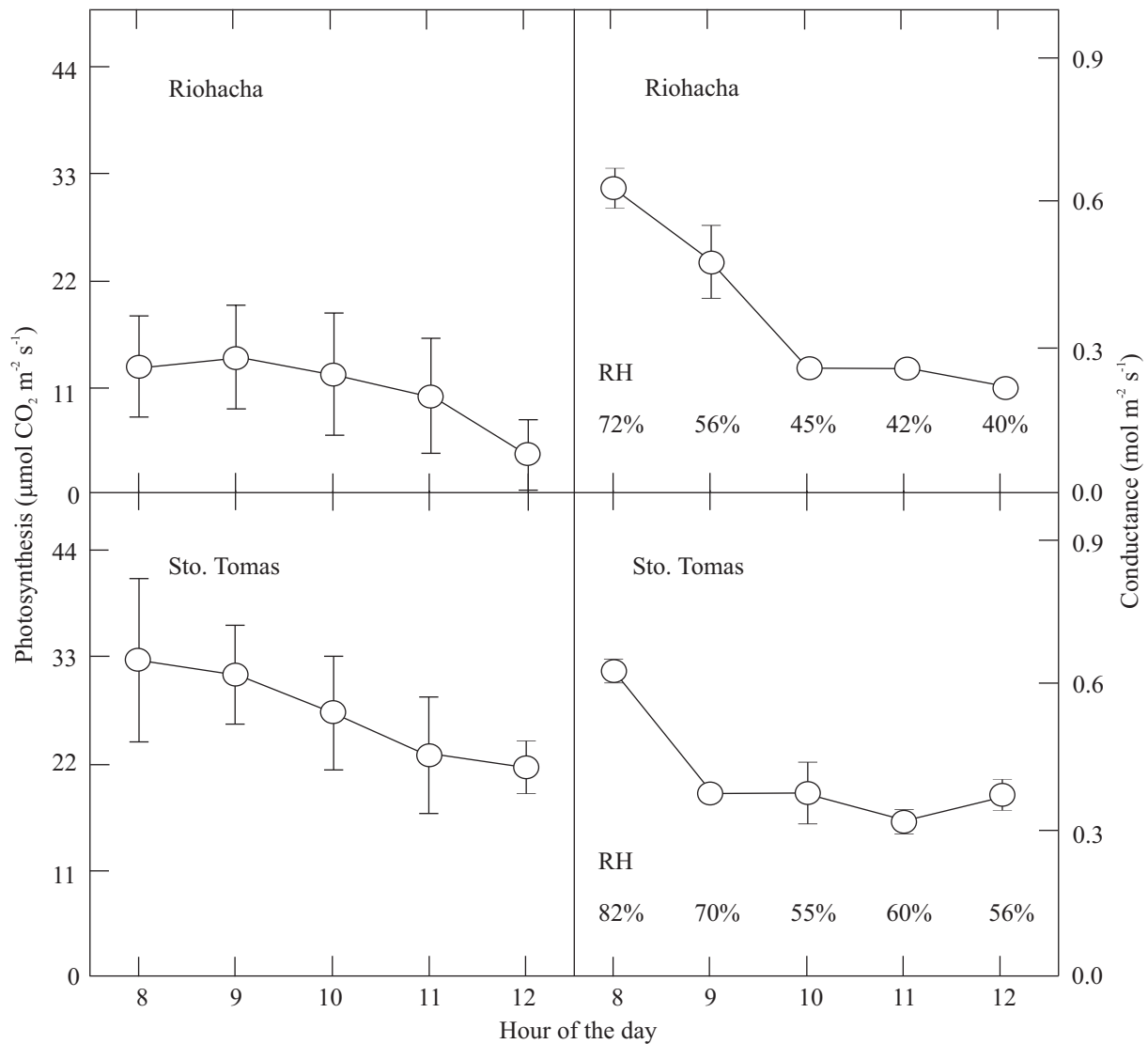


**Figure 6.** Response of field-grown cassava to prolonged midseason water stress. Cassava plants were deprived of water by covering the soil surface with white plastic sheets for three months, commencing 90 days after planting. Plants recovered from stress (see arrows in **A** and **B**) under rainfall and supplemental irrigation for the rest of the growth cycle. The control plants received normal rainfall plus supplemental irrigation. Leaf gas exchange was monitored with a portable infrared gas analyzer throughout the stress and recovery periods. **A.** Leaf photosynthesis during stress and recovery for leaves developed under stress. **B.** Stomatal conductance. **C.** and **D.** Photosynthesis and stomatal conductance for new leaves developed after stress was terminated. Source: CIAT, Cassava Physiology Section database (1991) Annual Report; El-Sharkawy (1993).

table as a variable for water availability (Okogbenin et al., 2003). These findings support the sound breeding strategy for developing cultivars for specific ecozones (Hershey and Jennings, 1992; El-Sharkawy, 1993; Iglesias et al., 1995; Jennings and Iglesias, 2002).

Plant ecophysiologicalists have proposed a sort of "classification/terminology" scheme based on mechanisms underlying plant adaptation to water deficits (for more information see for example, Levitt, 1980; Turner, 1986; Ludlow and Muchow, 1990). According to Turner (1986), plants that are able to endure long periods of water shortages while maintaining a high tissue water

potential are called drought tolerant. Cassava may fit among these types of plants. Nevertheless, Alves (2002), working with indoor-grown plants, found no significant accumulation of solutes and osmolytes in mature cassava leaves, and, hence, no occurrence of osmotic adjustment (for more information, see [http://www.generationcp.org/vw/Download/ARM\\_2005/SP3\\_Alves.pdf](http://www.generationcp.org/vw/Download/ARM_2005/SP3_Alves.pdf)). This finding further confirms that cassava stomatal control over plant water relations is the predominant defense mechanism protecting the leaf from severe dehydration, and, hence, it can be considered a stress avoidance mechanism (El-Sharkawy, 2006a). Similar stomatal reactions to

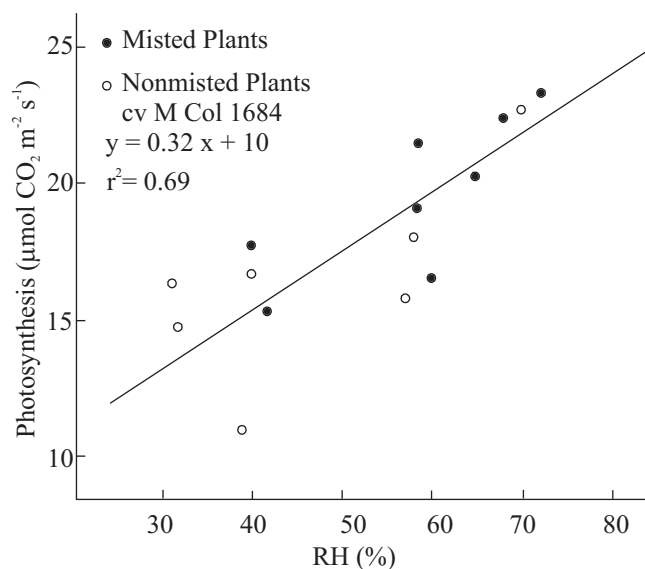


**Figure 7.** Leaf gas exchange as a function of time of measurement at Riohacha (semiarid) and Santo Tomas (seasonally dry). Data are averages of fourteen cultivars. RH: atmospheric relative humidity. Source: CIAT (1993); de Tafur et al. (1997b).

atmospheric and soil water deficits that strongly control water use, often coupled with deep rooting systems, were observed in drought-tolerant cultivars of other tropical perennial trees/shrubs as in *Coffea arabica* and *C. canephora* (Hernández et al., 1989; Pinheiro et al., 2005; DaMatta and Ramalho, 2006).

The discussed above plant traits and mechanisms that underlie cassava tolerance to prolonged drought have further implications for the possible expansion of adaptable cassava cultivars into marginal lands and under adverse climatic conditions. As a potential food

and feed crop for the tropical and subtropical regions most likely affected by global climate changes, cassava will probably become an important food-security source in developing countries where there are severe food shortages (Rosenzweig and Parry, 1994; Kamukondiwa, 1996; El-Sharkawy, 2005; IPCC, 2006). Rosenzweig and Parry (1994) pointed out that cereal crop production in the tropics and subtropics will possibly decrease in the near future because of global climate changes, hence, food shortages would be further aggravated in these regions.



**Figure 8.** The apparent photosynthetic rate of field-grown cassava as a function of atmospheric relative humidity. (●) Misted plants, (○) Nonmisted plants ('M Col 1684'). Soil was wet in both treatments. Source: Cock et al. (1985).

#### Selection for drought tolerance in cassava for seasonally dry and semiarid environments in Colombia

The physiological research, as discussed above, laid the foundation for improving the cassava genetic base, and for selection for drought tolerance in seasonally dry and semiarid environments where a significant portion of cassava production occurs (El-Sharkawy, 1993; Iglesias et al., 1995). A large group of cassava from the core germplasm collection was screened for leaf photosynthesis and productivity in seasonally dry and semiarid environments in Colombia.

*Evaluation of core germplasm for productivity and photosynthesis in seasonally dry environment at the southwest Andean mountains of Colombia:* In the 1986-1987 growing season, 127 CIAT cassava accessions, including cultivars, land races and breeding lines were screened on a private farm in the Patia Valle, Cauca Department, Colombia (600 m a.s.l., latitude 2°09'N, longitude 77°04'W, mean annual temperature 28°C with little seasonal variation, average atmospheric humidity about 70%). The soils in Patia Valley are heavy clay, and the farm was under continuous pasture grasses, mainly *Panicum maximum*, for the last 25 years. The trial was planted at a population density of 15,625 plant ha<sup>-1</sup> on 23

October 1986, with adequate fertilization. The site received about 700 mm of rain in 309 d, but from December 1986 to April 1987, the rainfall was much less than the potential evaporation which was greater than 5 mm d<sup>-1</sup>. The Patia Valley, lying between the central and western Andes mountains, is characterized by two wet periods (October-December and March-June), and with high solar radiation of about 22 MJ m<sup>-2</sup> d<sup>-1</sup>. The 1986-1987 season was particularly dry, with no rainfall recorded from June to August. The trial was harvested on 26 to 27 August 1987.

Measurements of single-leaf gas exchanges were made with a portable infrared gas analyzer (LI-COR model LI-6000) using central lobes of upper canopy leaves on several occasions between February to June 1987. At this stage of crop growth, LAI was near its peak, and storage root bulking rate was greatest, and, hence, both carbon source capacity and root-sink demand were near optimal. Measurements were always made from 0900 to 1300 h when the solar irradiance exceeded 1000 μmol m<sup>-2</sup> s<sup>-1</sup> of PAR. Leaf water potential was determined with the standard pressure chamber technique (Scholander et al., 1965) on lobes from the same leaves used for gas exchange. Values for leaf water potential ranged from -1.0 to -1.5 MPa, across varieties and measurement dates. Nitrogen, phosphorus and potassium contents were also determined on the same measured leaves (El-Sharkawy et al., 1990).

Across all accessions, both fresh total plant biomass and dried root yield were highly significantly and positively correlated with average leaf photosynthetic rate, and the correlation was higher in the high and medium top weight varieties than in the low top ones. These results indicate that, on the one hand, at high level of light interception (i.e., near optimum LAI in high and medium top weight), there was a direct relationship between productivity and leaf photosynthesis. On the other hand, at lower light interception because of lower than optimal LAI in the low top genotypes, the relation is weaker and light interception appears to be the predominant factor in determining productivity. Thus, when both canopy light interception and root-sink demand for carbohydrate are not limiting, productivity correlates well with leaf photosynthesis, as measured in the field (El-Sharkawy and Cock, 1990; El-Sharkawy et al., 1989, 1990).



**Table 4.** Effect of water stress imposed at different stages of growth on storage root yield and shoot biomass at 12 months after planting, and on mean leaf area index (Mean LAI) over the growth cycle for four cassava cultivars grown at Santander de Quilichao, Cauca, Colombia in 1991-1992 and 1992-1993. Data are means of two years. Harvests were made 12 months after planting. Source: El-Sharkawy and Cadavid (2002).

Cultivar	Treatment				Treatment				Treatment			
	Control	Early†	Mid- season†	Terminal†	Control	Early	Mid- season	Terminal	Control	Early	Mid- season	Terminal
	Dry root yield (t ha <sup>-1</sup> )				Dry shoot biomass (t ha <sup>-1</sup> )				Mean LAI			
CM 507-37	14.0	11.1	11.3	11.1	6.0	2.7	5.6	5.3	2.3	1.3	1.8	2.3
CM 523-7	13.8	12.8	12.1	9.7	5.3	4.2	5.2	4.5	2.3	1.4	1.3	2.0
CMC 40	10.0	10.4	12.1	14.6	7.8	3.9	5.7	6.7	1.7	1.1	1.1	1.7
M Col 1684	13.6	10.3	12.5	11.5	5.0	2.2	4.0	4.3	1.8	1.1	1.3	1.8
Average	<b>12.9</b>	<b>11.2</b>	<b>12.9</b>	<b>11.7</b>	<b>6.0</b>	<b>3.3</b>	<b>5.1</b>	<b>5.2</b>	<b>2.0</b>	<b>1.2</b>	<b>1.4</b>	<b>2.0</b>
LSD ( <i>P</i> = 0.05)												
Treatment	NS				0.8				0.3			
Treatment x Cultivar	2.7				1.4				0.5			

NS = non-significant, *P* > 0.05; †Early stress-plants were deprived of water from 2-6 months after planting; Mid-season stress-plants were deprived of water from 4-8; Terminal stress-plants were deprived of water from 6-12 months. Before imposing water stress by covering the soil with plastic sheets, the soil-water to 2-m depth was brought to field capacity by irrigation. During the water stress period, plants depended on stored water only which was about 200 mm in the 2-m depth. The total extracted water during stress varied from ~150 to 180 mm, depending on cultivar and treatment.

**NOTE:** (1) the lack of significant difference due to water treatment in root yield across cultivars; (2) the significant reduction in shoot biomass and Mean LAI due to water stress, particularly in early stress; (3) the significant treatment x cultivar interactions; (4) the highest (14.6) and lowest (9.7) yields were obtained under terminal stress for cv. CMC 40 and CM 523-7, respectively; (5) cultivars CM 507-37 and M Col 1684 showed intermediate responses to water stress. Because of reductions in shoot biomass, and consequently reductions in total nutrient uptake, in early and mid-season water stress, average nutrient-use efficiency (kg dry root per kg total nutrient uptake) was increased by 14 to 40%, depending on water treatment and element (El-Sharkawy et al., 1998; El-Sharkawy and Cadavid, 2002). Under terminal stress there were no changes in nutrient-use efficiency because the peak nutrient uptake occurred at 5-6 month after planting and before the start of stress. Early stress seems beneficial in low-fertility soils under bimodal rainfall patterns. In this case, cassava should be planted toward the end of the rainy period, pass into a dry period, and then into a second wet period. Even cassava shed most of its leaf canopy under prolonged drought, it recovers quickly in subsequent wet conditions forming reasonable canopy with higher leaf photosynthetic rates (El-Sharkawy et al., 1992b; El-Sharkawy, 1993, 2006a; Cayón et al., 1997).

Sixteen clones were selected from the many screened accessions on the basis of their high-yield performance, and were planted on 13 April 1988, in another adjacent private farm in the Patia Valley, and at a population density of 10,000 plants ha<sup>-1</sup>. A split-block design with four replications was used to allow for two fertilization treatments, i.e., (1) without fertilization; (2) with 50, 100 and 100 kg NPK ha<sup>-1</sup>. The size of the plot per clone was 25 m<sup>2</sup>. The crop received about 950 mm of rain during the growing cycle of 308 d, with 560 mm out of the total rainfall occurring in October and November 1988, which resulted in a significant amount of water runoff. On 14-16 February 1989, the nine central plants per plot were harvested to determine biomass and root yield weight. Measurements of single-leaf gas exchanges were made only once per day on 29 August to 7 September 1988, with an LCA-2 portable infrared gas analyzer (Analytical

Development Co., UK) that operates in an open-end system, in contrast to the LI-COR 6000 that operates in a closed fashion system. Across all blocks and fertilizer treatments, 35 fully expanded upper-canopy leaves were measured per cultivar. A small leaf chamber (Parkinson Broad Leaf Model) was clamped over the middle portion (6.25 cm<sup>2</sup> leaf surface area), in contrast to the 4-L leaf chamber used with the LI-COR closed system where the whole lobe of cassava leaf was measured for gas exchanges. All measurements were made from 0800 to 1300 h with solar irradiance exceeding 1000 μmol m<sup>-2</sup>s<sup>-1</sup> of PAR. Normal air with 320 ± 10 μmol mol<sup>-1</sup> CO<sub>2</sub> was drawn from above canopy using a vertically mounted 4-m glass-fiber probe connected to a pump.

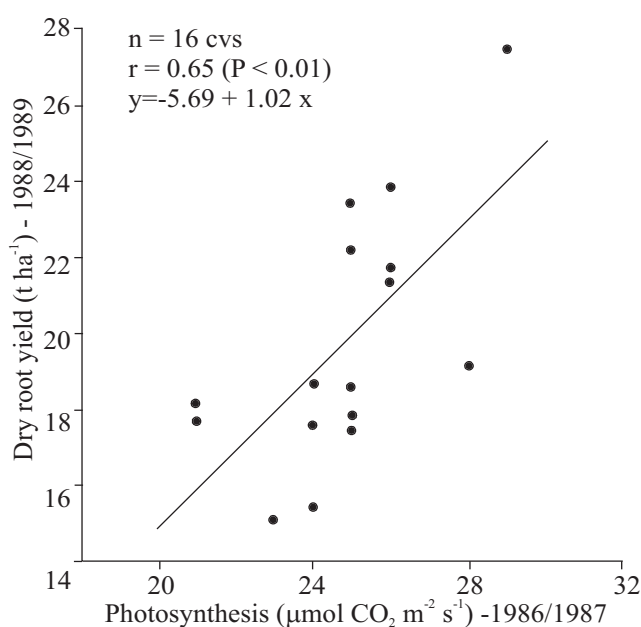
Since no significant fertilizer effects were observed in root yield and gas exchange rates, data were pooled. Average root yields were higher than those in the 1986-

1987 preliminary screening trial, and this was mainly attributed to the higher rainfall in 1988-1989, as well as to the smaller group of selected high-yielding clones. The mean dry root yield among the 16 cultivars ranged from 15 to 27 t ha<sup>-1</sup>, indicating the high yield potential in cassava when grown in near optimal environments. In this trial with nearly 9000 m<sup>2</sup> land including borders, the overall average dry root yield harvested from the whole area exceeded 20 t ha<sup>-1</sup>.

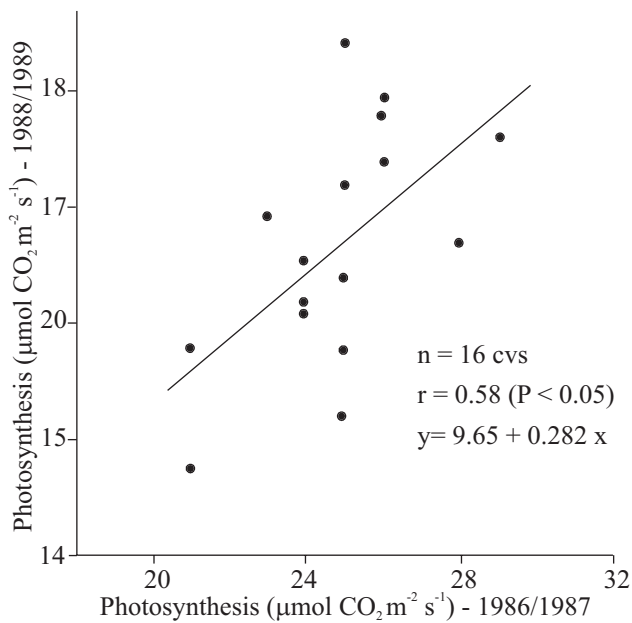
Despite differences in rainfall between the two growing seasons, the leaf photosynthetic rates measured in 1986-1987 season were highly significantly and positively correlated with the dry root-yield of the 1988-1989 season (Figure 9). Furthermore, average leaf photosynthetic rates, as measured only once with the LCA-2 in the 1988-1989 season, was significantly correlated with rates measured over a more extended period of time in the 1986-1987 season with the LI-COR closed system (Figure 10). The dry root yield and the average leaf photosynthesis of the 1988-1989 season crop were also significantly correlated (Figure 11). These data clearly demonstrate the consistent relation over years between upper canopy single-leaf photosynthesis, as measured in the field, and productivity in cassava.

The relation between leaf photosynthesis and productivity was mainly due to nonstomatal factors (i.e., due to biochemical/anatomical leaf characteristics), as demonstrated by the negative significant correlation between yield and intercellular CO<sub>2</sub> concentration (C<sub>i</sub>) (El-Sharkawy et al., 1990). This conclusion is further substantiated by the significant positive correlation between yield and photosynthetic nitrogen-use efficiency (PNUE = CO<sub>2</sub> uptake/ unit total leaf nitrogen, Figure 12). Leaf anatomical characteristics that may affect the amount and distribution of photosynthetic machinery can play a significant role in leaf photosynthesis. But since yield is significantly correlated with PNUE, it appears, therefore, that biochemical factors affecting photosynthesis, such as activities of photosynthetic enzymes, are more important in this case. Leaf photosynthetic rates of various cassava varieties subjected to water stress in the field were significantly and positively correlated with the activity of the C<sub>4</sub> enzyme PEPC activity in extracts of the same measured leaves (El-Sharkawy, 2004). Table 5 (El-Sharkawy et al.,

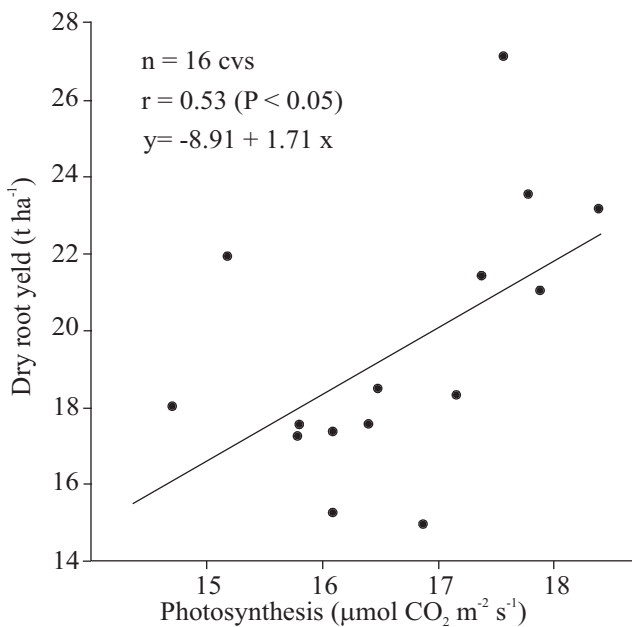
2008) presents correlation coefficients and regressions between yield, photosynthetic characteristics, and PEPC activity in 18 varieties selected from the preliminary trial in Patia. There were significant correlations between yield, photosynthetic characteristics and PEPC activity. Such activity was highly significantly correlated with P<sub>N</sub> and PNUE. Moreover, PEPC activity in cassava was much greater than that observed in typical C<sub>3</sub> plants and about 10-30% of the activity in typical C<sub>4</sub> species such as maize and sorghum (El-Sharkawy et al., 1989; El-Sharkawy and Cock, 1990; El-Sharkawy, 2004, 2006a). Also, it is possible that differences in leaf photosynthesis within cassava germplasm could be due partly to differences in characteristics of the C<sub>3</sub> enzyme, Rubisco. Paul and Yeoh (1987) reported wide variation in kinetic properties of cassava Rubisco. Values of K<sub>m</sub> (CO<sub>2</sub>) for 16 cassava varieties ranged from 7.8 to 14.0 μM CO<sub>2</sub>, while K<sub>m</sub> (RuBP) values ranged from 7.5 to 24.8 μM RuBP. Wide variation was also found in activities of Rubisco among cassava genotypes (López et al., 1993; El-Sharkawy, 2004, 2006a). Thus, selection for high photosynthetic rates and high enzyme activity would be beneficial for breeding improved cassava varieties, particularly under drought



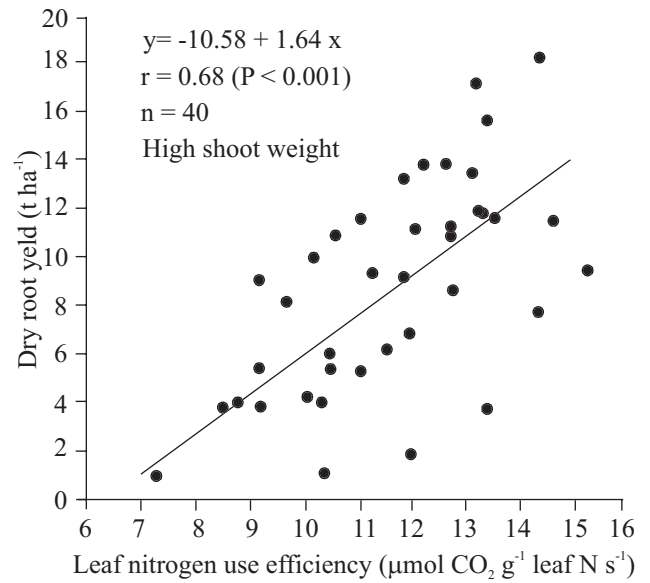
**Figure 9.** Relationship between the 1988/1989 dry root yield and the single-leaf photosynthesis measured in the 1986/1987 season. Data of yield are averages of eight replications, sixteen cultivars. Source: El-Sharkawy et al. (1990).



**Figure 10.** Relationship between the 1988/1989 leaf photosynthesis measured once with the open-end LCA-2 apparatus, at 4 months after planting and the 1986/1987 rates measured with the LI-600 closed-circuit apparatus on three occasions at 4-6 months after planting. Source: El-Sharkawy et al. (1990).



**Figure 11.** Relationship between dry root yield and leaf photosynthesis of the 1988/1989 season. Data of yield are averages of eight replications, sixteen cultivars. Source: El-Sharkawy et al. (1990).



**Figure 12.** Relationship between dry root yield and leaf nitrogen use efficiency in field-grown cassava. Leaf nitrogen use efficiency values were calculated from leaf CO<sub>2</sub> exchange measurements and total leaf nitrogen concentrations. Data for 40 cultivars with high shoot weight. Source: El-Sharkawy, (2004).

conditions. Molecular biologists, along with plant breeders, physiologists and biochemists, should participate in screening for genetic variation in photosynthetic characteristics and in identifying potential genotypes as a genetic source for crossing in breeding programs. Interdisciplinary/interinstitutional collaboration should enhance progress and ensure efficiency in science output, and, hence, increase the benefit/cost ratio of research.

*Evaluation of core germplasm in both seasonally dry and semiarid environments in northern coast of Colombia:* Two field trials were conducted during the 1992-1993 season in two locations at the northern coast of Colombia using two groups of cassava clones selected from the CIAT core germplasm. One trial was conducted on a private farm at Santo Tomas, Atlantic Department (14 m a.s.l., latitude 10°57'N; longitude 74°47'W). At this site the mean annual rainfall of 830 mm is 50% of the mean annual pan evaporation of 1650 mm, with a rainy period from May to November and a dry period from December to April. The soil at the site is sandy (>80% sand) with low water holding capacity, very low in organic matter and

**Table 5.** Correlation coefficients and regression equations for various plant trait combinations in 18 cultivars selected from the preliminary-screened 127 in Patia, Cauca, Colombia, 1986-1987. Leaf photosynthetic characteristics were determined in upper canopy leaves from 5-8 month-old-plants. Leaf nitrogen content and PEPC activity were determined in upper canopy leaves from independent leaf samples from 5-month-old-plants. Measurements were made during dry period.  $n = 18$ . Source: El-Sharkawy et al. (2008).

Trait combination		Correlation coefficient ( $r$ )	Regression equation ( $y = a + bx$ )
x	y		
$P_N$	Yield	0.500*	Yield = $0.178 + 0.047 P_N$
PNUE	Yield	0.481*	Yield = $0.605 + 0.062 \text{PNUE}$
PEPC	Yield	0.547*	Yield = $0.804 + 0.057 \text{PEPC}$
$g_m$	Yield	0.479*	Yield = $-0.066 + 0.014 g_m$
PEPC	$P_N$	0.597**	$P_N = 18.43 + 0.69 \text{PEPC}$
PEPC	$g_m$	0.532*	$g_m = 83.5 + 2.0 \text{PEPC}$
PEPC	PNUE	0.698**	PNUE = $6.42 + 0.58 \text{PEPC}$

\*, \*\* indicate level of significance at  $P = 0.05$  and  $0.01$ , respectively.

$P_N$  = net leaf photosynthetic rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ); PNUE = photosynthetic nitrogen-use efficiency [ $\text{mmol CO}_2 \text{ kg}^{-1}$  (total leaf nitrogen)  $\text{s}^{-1}$ ]; PEPC = phosphoenolpyruvate carboxylase activity ( $\mu\text{mol kg}^{-1} \text{ FM s}^{-1}$ );  $g_m$  = mesophyll conductances to  $\text{CO}_2$  diffusion ( $\text{mmol m}^{-2} \text{ s}^{-1}$ ); Yield = dry root yield ( $\text{kg m}^{-2}$ ).

Values of cultivars (means), and ranges:  $P_N$  (25.1), 21 to 30.6; PNUE (12.1), 9.4 to 16.2; PEPC activity (9.7), 6.3 to 14.0;  $g_m$  (103), 93 to 126; Yield (1.36), 1.00 to 1.83.

**Note:** The significant correlations between PEPC activity and photosynthetic characteristics and yield of cassava point to the importance of the enzyme as a desirable selectable trait for cultivar improvement, particularly under stressful environments.

low in nutrients. The second trial was conducted at a site of a religious school for the native young students (Aremasain) near Riohacha, Guajira Department (4 m a.s.l., latitude  $11^\circ 32' \text{N}$ ; longitude  $72^\circ 56' \text{W}$ ). At that site the mean annual rainfall of about 560 mm is 25% of the mean annual pan evaporation of 2300 mm. The rainfall distribution pattern in this region is characterized by a short rainy period from September to November, a dry period from December to April, and a second low-rainfall period from May to August. The soil in that site is sandy (> 80% sand) with low water holding capacity, very low in organic matter and nutrients. In both trials, no chemical fertilizer was applied.

Healthy stem cuttings (20 cm long) of the tested cultivars were planted on 25 September 1992 (Santo Tomas, Atlantic) and on 19 September 1992 (Riohacha, Guajira) on flat places of disked land at a 1 m by 1 m distance and in 5 x 5 m plots with four replications in a randomized complete-block design. The eight central plants from each plot were harvested for determination of yields on 4 August 1993 (Riohacha) and 5 August 1993 (Santo Tomas).

Under the above-mentioned stressful environments, average oven-dried root yield was  $6.7 \text{ t ha}^{-1}$  at the seasonally dry location (yield ranged among cultivars

from  $5.8$  to  $7.6 \text{ t ha}^{-1}$ ), whereas at the semiarid location overall average yield was  $2.3 \text{ t ha}^{-1}$  (yield ranged among cultivars from  $0.4$  to  $3.3 \text{ t ha}^{-1}$ ). These levels of productivity, without fertilization and with severe prolonged drought, illustrate again the high adaptability of cassava to adverse atmospheric and edaphic conditions. Moreover, the crop not only survived but also produced reasonably well, where other major staple food crops like tropical cereals would not be able to compete with cassava. The most drought-tolerant tropical cereals such as grain sorghums and millets (Blum and Sullivan, 1986) perhaps would fail to produce under the semiarid conditions experienced in these trials. Nevertheless, because of the severe shortage of rainfall in the semiarid environment, root dry matter content was lower (less than 30%) than in seasonally dry environments. In practice, however, such as in northeastern Brazil with mean annual rainfall less than 700 mm, the crop is allowed to go into a second wet cycle that leads to higher yields as well as higher root dry matter content.

Measurements of leaf gas exchanges were made with an LCA-2 portable infrared gas analyzer during several days from February to March, 1993. All measurements were made on upper canopy leaves (four leaves per

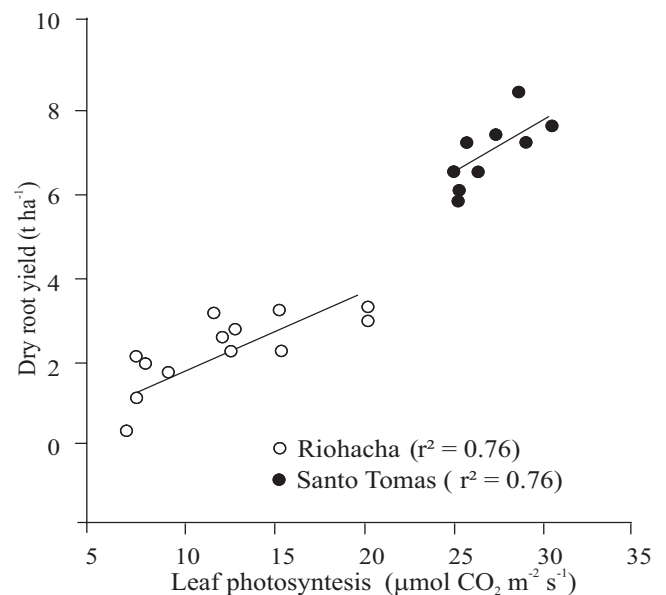
cultivar per replication with a total of 16 leaves) between 0800 h and 1200 h local time with a solar irradiance higher than  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Measurements were taken during the dry period 4-5 months after planting at air temperatures within the leaf cuvette ranging from 29 to  $37^\circ\text{C}$ , depending on time and date of measurements. This range of temperatures is near the optimum for photosynthesis in cassava as measured under controlled laboratory conditions (El-Sharkawy and Cock, 1990; El-Sharkawy et al., 1992a).

Overall average photosynthetic rates across cultivars were much higher at the seasonally dry site than at the semiarid one, with the highest rates observed early in the morning and the lowest at midday (Figure 6) (de Tafur et al., 1997b). Leaf conductance to water vapor showed the same trend, indicating the striking effect of air humidity on stomatal opening as previously observed under controlled laboratory conditions (El-Sharkawy and Cock, 1984, 1986; El-Sharkawy et al., 1984, 1985). These photosynthetic rates are much lower than the maximum rates (above  $40 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) that are normally observed in field-grown cassava in wet soils and with high atmospheric humidity (El-Sharkawy et al., 1992a, 1993). However, compared with other field crops, cassava is more photosynthetically active under severe prolonged drought, an advantage that underlies its remarkable productivity and ability to endure harsh environments. Thus, it is beneficial to select for higher photosynthetic capacity, combined with other desirable plant traits such as longer leaf life (better leaf retention and duration, Lenis et al., 2006) and deeper and extensive fine root systems in order to enhance growth and yield in dry areas.

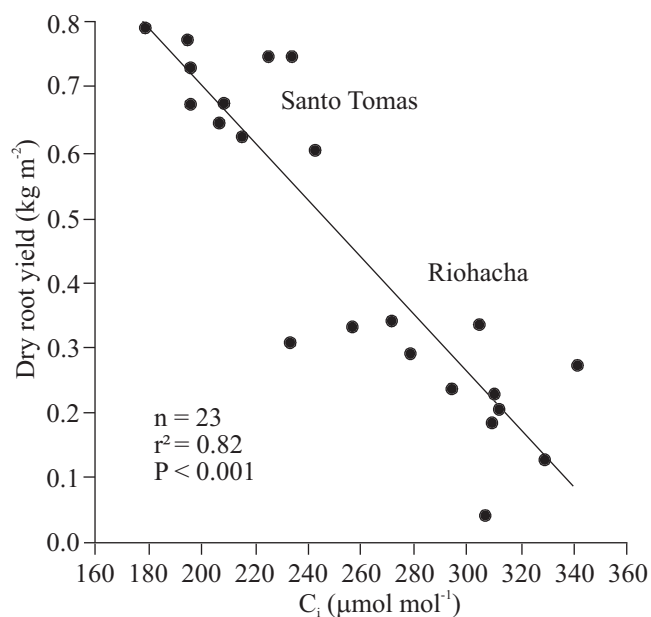
In both environments, dry root yield was highly significantly and positively correlated with average leaf photosynthetic rate (Figure 13,  $r^2 = 0.76$ ,  $P < 0.01$ ) (CIAT, 1995; de Tafur et al., 1997b). Moreover, dry root yield was highly significantly and negatively correlated with  $C_i$  (Figure 14,  $r^2 = 0.82$ ,  $P < 0.001$ , de Tafur et al., 1997b), indicating that the relation is due mainly to nonstomatal factors controlling leaf photosynthesis (i.e., biochemical/anatomical factors). These results corroborate other findings in humid and sub-humid/seasonally dry environments, as discussed above (El-Sharkawy et al., 1990, 1993; Pellet and El-Sharkawy, 1993; El-Sharkawy, 2006a). The results also point to the importance of

utilizing genetic variations in photosynthetic enzyme characteristics as selection criteria in cassava breeding, particularly for improved genotypes targeted for dry environments. The  $C_4$  PEPC, in particular, plays a significant role in cassava photosynthesis, when the numerous abaxial stomata close in hot-dry environments. Under this situation, PEPC recycles respiratory  $\text{CO}_2$ , and, hence, dissipates excess solar energy and obviates photoinhibition of the photosynthetic process.

*Breeding for drought tolerance in cassava under the semiarid conditions of northeastern Brazil:* Besides being, for millennia, the main geographical site for the origin of cassava, the center for its genetic diversity and for its domestication (Allem, 2002), Brazil is the largest cassava producer in Latin America. According to FAOSTAT (1999) (cited by Henry and Hershey, 2002), the 1999 area harvested under cassava in Brazil was about 1.54 million ha, about 21% less than that in 1990 and the total fresh root production was 20.2 million tons (12.7 % of world 1999 estimated production of about 158 million tons). The estimate of root yield across the country was  $13.1 \text{ t ha}^{-1}$  for 1999, slightly higher than that in 1990 (about  $12.6 \text{ t ha}^{-1}$ ). On the one hand, one reason behind the



**Figure 13.** Relationships between root yield and leaf photosynthesis of several cassava clones grown in seasonally dry (Santo Tomàs, Atlàntico) and semiarid (Riohacha, Guajira) environments. Source: CIAT (1995) Report.



**Figure 14.** Relationship between dry root yield and intercellular CO<sub>2</sub> concentration (C<sub>i</sub>) for two groups of cassava cultivars grown under rain-fed conditions at Riohacha (semi-arid) and Santo Tomas (seasonally dry). The C<sub>i</sub> values were calculated from leaf gas fluxes via standard Gaastra equations: the higher photosynthetic rates, the lower C<sub>i</sub> values. Regression equation: yield = 1.52 - 0.004C<sub>i</sub>; r<sup>2</sup> = 0.82 (P < 0.001). Source: de Tafur et al. (1997b).

decrease in acreage, and consequently the reduction in total production, was the pattern of decreasing cassava cultivation in the most favorable environments in southern Brazil (El-Sharkawy, 1993). On the other hand, in the more marginal regions of the semiarid northeastern Brazil, the area under cassava production expanded rapidly and now may account for more than 50% of the total Brazilian production. This trend strengthened the importance of improving the genetic base of cassava, and for breeding new cultivars more adapted to the severe water stress conditions prevailing in that region. This objective was further strengthened by the knowledge of cassava's inherent potential for drought tolerance and the newly acquired basic physiological information and insights about the mechanisms underpinning such tolerance.

In late 1980 and early 1990, breeding efforts at CIAT were further integrated with the Brazilian national institutions involved in cassava research, mainly the federal research organizations of EMBRAPA and

CNPMPF, with headquarters at Cruz das Almas, Bahia State (Fukuda et al., 1992-1993). Also, collaboration with IITA, Nigeria, took place at the same time. As the crop physiologist at CIAT, I participated, along with CIAT breeders and the Brazilian national cassava team, in the initiation of a research project for cassava breeding in northeastern Brazil that was supported by the International Fund for Agricultural Development, Rome (El-Sharkawy, 1993). Based on the available meteorological data, four relevant sites were pre-selected for screening cassava germplasm in northeastern Brazil, namely: (1) Itaberaba, Bahia (270 m a.s.l., latitude 12°31'S). At this site, mean annual rainfall is about 718 mm, with a continuous rain throughout the year, but with two wet cycles. From January to April total rainfall is about 332 mm. There is a shorter wet cycle from November-December with a total rainfall of 200 mm. The rest of the year is considered dry as the monthly rainfall oscillated between 20 to 40 mm, which is far below the potential evaporation. (2) Quixadá, Ceará (179 m a.s.l., latitude 4°57'S). At this site, mean annual rainfall is about 677 mm, with only a four-month wet cycle (from February to May) with a total rainfall of 542 mm. The rest of the year is extremely dry, as monthly rainfall oscillated between zero to 45 mm. (3) Petrolina, Pernambuco (376 m a.s.l., latitude 9°22'S). At this site, mean annual rainfall is about 400 mm, with monthly distribution (mm) as follows: 50 in January, 78 in February, 92 in March, 43 in April, 7 in May, 4 in June, 2 each from July to September, 9 in October, 45 in November, 64 in December. This site is the driest among the pre-selected sites, as illustrated by the pattern of rainfall distribution. (4) Araripina, Pernambuco (816 m a.s.l., latitude 7°32'S). This site is the wettest among the pre-selected sites with mean annual rainfall of about 820 mm. The rainfall distribution pattern is very similar to that in Petrolina, but with the three wetter months having a total rainfall of 422 mm (January 114, February 134, March 174). The rest of the year was considered dry, as indicated by the monthly rainfall distribution that oscillated between zero and 63 mm. The soils in these sites are sandy with low water holding capacity in addition to being very low in fertility.

Cassava germplasm (500 clones) originating from northeast Brazil and the north coast of Colombia was initially screened at these four sites for yield, harvest

index, root dry matter content, cyanogenic glucosides level (expressed in total hydrocyanic acid, HCN, concentration in storage root parenchyma) and resistance to mites. In general, in the 1991-1992 growing season, cassava at all sites suffered from a more severe drought than normal, with total annual rainfall less than 200 mm in Petrolina, less than 500 mm in Araripina, less than 360 mm in Quixadá. Only at Itaberaba was rainfall about 853 mm, more than normal (Fukuda et al., 1992-1993). Despite these harsh environments, a large number of accessions persisted and produced, while some failed. Better drought-adapted clones established full canopy after four months and retained leaf area up to eight months after planting (Fukuda et al., 1992-1993; El-Sharkawy, 1993). In Table 6 the results of the preliminary screening trials as overall averages of the four sites are summarized. Several accessions of Brazilian origin were selected with good yield potential that ranged from 13 to 18 t ha<sup>-1</sup> fresh roots with mean 25% dry matter. Harvest index ranged from 0.45 to 0.55. There was tolerance to prolonged drought, as indicated by better leaf retention and duration during most of the cropping cycle. Low HCN content was in root parenchyma, and they ranged from 53 to 100 mg kg<sup>-1</sup> fresh root, which are acceptable levels for fresh root consumption. Mite resistance scores ranged from 3.3 to 2.7, based on a visually assessed scale from 5 (highly susceptible) to 1 (highly resistant).

These preliminary trials laid the foundations for a further expanding of the breeding project based on a scheme for producing hybrids via crossing among various selected clones with a range of desirable traits under semiarid conditions (Fukuda et al., 1992-1993). Further on-farm trials involving farmers in the process of evaluation of breeding materials have resulted in a few selected genotypes with higher yields, compared to local checks (Table 7). When left for a second wet cycle in semiarid low-rainfall locations, fresh yields more than doubled (from an average yield of 14 t ha<sup>-1</sup> at 12 months to 35 t ha<sup>-1</sup> at 18 months). The dry matter contents in fresh roots increased from 25% at 12 months to 35% at 18 months, which led to more than three-fold increases in dry root yields (from an average of 3.5 t ha<sup>-1</sup> at 12 months to 12.2 t ha<sup>-1</sup> at 18 months). Farmers adopted some of these improved genotypes and started multiplying planting material even before being officially released. In

these semiarid environments drought-tolerant grain crops such as sorghum and millets (Blum and Sullivan, 1986) will fail to produce as much, indicating the comparative advantages of cassava. This research is a remarkable example of interdisciplinary/interinstitutional collaborative efforts that serve the needs of some of the poorest farmers in the tropics. Consequently, a follow-up collaborative research project supported by the CGIAR Generation Challenge Program was conducted by EMBRAPA/CNPMPF, Brazil, CIAT, Colombia, IITA, Nigeria, and Cornell University, USA (see: [http://www.generationcp.org/vw/Download/Competitive\\_Grant\\_Proposals/3\\_ALVES.pdf](http://www.generationcp.org/vw/Download/Competitive_Grant_Proposals/3_ALVES.pdf)). More than 20 new genotypes tolerant to drought were selected (see: [http://www.generationcp.org/vw/Download/ARM\\_2005/SP3\\_Alves.pdf](http://www.generationcp.org/vw/Download/ARM_2005/SP3_Alves.pdf)).

## FUTURE WORK

Two areas of research and development need to be addressed on the potential use of cassava as a mainstay crop tolerant to extreme water deficits and to marginal lands in the tropics and subtropics where severe drought prevails and shortages of food and feed are chronic, particularly in Sub-Saharan Africa: (1) Through the use of modern molecular biology tools, more basic research on cassava biochemical photosynthetic characterization should be done to search for genetic diversity within cultivated cassava and wild *Manihot* species in order to identify genetic sources with high photosynthetic rates and enhanced activities of key photosynthetic enzymes, focusing on PEPC and C<sub>3</sub>-C<sub>4</sub> traits (El-Sharkawy and de Tafur, 2007; El-Sharkawy et al., 2008). The use of molecular markers and marker assisted selection should facilitate and enhance the conventional breeding process for drought-tolerance in cassava (Setter and Fregene, 2007). Also, the molecular basis for tolerance to water stress and identification of possible controlling genes should be investigated using contrasting germplasm (e.g., Lokko et al., 2007). This line of research should be internationally supported within an interinstitutional/interdisciplinary collaborative network, including research institutes in developed countries. (2) National programs, perhaps supported with the Geographical Information Systems (GIS), should make the necessary

**Table 6.** Clones (harvested at 12 months) with good level of adaptation to four screening sites in semiarid northeastern Brazil. Values are averages of all sites. Source: CIAT/CNPMF breeding database 1992; El-Sharkawy (1993).

Brazil accession code	Fresh root yield (t ha <sup>-1</sup> )	HI *	Root dry matter content (%)	HCN content (mg kg <sup>-1</sup> fresh roots)‡	Mite resistance score †
BGM 538	18	0.50	30.1	78	2.9
BGM 146	17	0.51	28.0	85	3.0
BGM 178	16	0.44	29.1	95	3.0
BGM 549	16	0.42	28.6	72	3.1
BGM 537	15	0.48	30.4	72	2.7
BGM 254	15	0.50	28.0	90	2.9
BGM 544	14	0.55	29.1	95	3.1
BGM 153	14	0.45	28.0	100	3.1
BGM 598	13	0.47	29.0	53	2.7
BGM 491	13	0.46	27.7	60	3.3
Overall mean of 500 clones	<b>9</b>	<b>0.40</b>	<b>25.1</b>	<b>75</b>	<b>3.3</b>

\* = Harvest index means the fresh root yield divided by fresh total harvested biomass excluding fallen leaves; † = Mite resistance score: 1 (highly resistance) to 5 (highly susceptible); ‡ = Total hydrocyanic acid content in parenchyma of peeled roots. The clones with HCN content less than 100 mg kg<sup>-1</sup> FM are considered safe for human consumption after fresh cooking. Higher levels of HCN are hazardous for human health if consumed without proper processing to eliminate most of the HCN.

mapping of additional new lands and suitable climatic conditions for potential expansion in cassava production where other staple food crops will probably fail to produce. This effort should be backed up by developing the necessary adapted cultivars endowed with early storage root filling characteristics (i.e., early bulking) and better leaf retention (Lenis et al., 2006) and duration coupled with resistance to pests and diseases. Agronomic/physiological research in the area of plant-soil-water relations and plant nutrition on the newly bred cultivars would provide the technical knowledge needed for cropping systems and natural resources managements. Crop modeling, based on sound field research, should play a role in this case (El-Sharkawy, 2005).

## CONCLUSIONS

The research on cassava summarized here illustrates the effectiveness and utility of ecophysiological research in improving the genetic base and in developing genotypes more adaptable to drought in the marginal environments in the tropics. Linking and integrating physiological research with breeding efforts within a commodity-oriented multidisciplinary research team at CIAT, and in collaboration with national programs, were pivotal in delivering the needed information and

improved technology. Plant traits related to productivity and to tolerance to water stress, such as high leaf photosynthetic capacity and longer leaf life and duration, extensive fine rooting systems and stomatal control of water losses, were identified and selected for parental materials used in breeding for improved and more adaptable genotypes. Furthermore, the research has revealed important information on the physiological mechanisms underlying cassava productivity and tolerance to prolonged drought that should help to develop better crop management in both favorable and stressful environments. More research is needed to elucidate further the biochemical and molecular characteristics of cassava photosynthesis in relation to productivity, particularly under stress. This would require essential changes in the current counterproductive policy of the international research system, which is based on short-term research projects that do not ensure needed solutions to farmers problems. This policy should be reversed and replaced by the previously adopted and more effective long-term core funding of interdisciplinary and integrated research approach (El-Sharkawy, 2006a,b). National programs should be responsible for conducting the applied and adaptive research aspects that are required for fulfillment of their national needs.

Across institutions and countries, collaborative



**Table 7.** Clones [(harvested at 12 and 18 months (M)] with good level of adaptation at the semiarid screening site in Quixadá, Ceará, northeastern Brazil, 1996. Source: CIAT/CNPMF breeding database (1996).

Brazil accession coode	Fresh root yield		Dry root yield		Dry matter content in roots	
	(t ha <sup>-1</sup> )				(%)	
	12 M.	18 M.	12 M.	18 M.	12 M.	18 M.
BGM 649	14.9	32.0	4.7	11.5	31.8	35.7
BGM 651	10.7	30.2	3.2	10.0	29.9	33.2
BGM 814	10.2	36.1	2.5	13.7	24.1	37.8
BGM 834	23.8	39.8	5.7	12.7	24.2	31.8
BGM 867	11.8	32.2	2.8	11.5	23.4	36.0
BGM 876	14.6	38.0	3.6	13.7	24.5	36.1
BGM 924	13.5	37.0	2.3	12.5	17.3	33.7
Mean of selections	<b>14.2</b>	<b>35.0</b>	<b>3.5</b>	<b>12.2</b>	<b>25.0</b>	<b>34.9</b>
Trial mean	12.7	26.6	3.2	9.2	25.2	34.5
Check varieties mean	7.1	27.8	1.7	9.8	23.8	35.3

**Note:** Farmers participated in the evaluation process and selected three clones with high yield and high dry matter content, and multiplied their planting material even before being officially released. Farmers' participation was crucial in enhancing the selection process and in speeding up adoption and diffusion of improved technology. The large increases in yield and in dry matter content at 18 months were attributed to the rainfall received in the last six months. At Quixadá, long-term mean annual rainfall is less than 700 mm, 80% falling mostly in 3-4 months and the rest of the year is dry coupled with hot climate that renders effective rainfall for growth to be less than 500 mm [total annual radiation = 8130 MJ m<sup>-2</sup>, mean annual temperature = 27°C, potential annual evapotranspiration = 2369 mm (El-Sharkawy, 1993)]. The soil at this site is sandy (> 80% sand) with low water holding capacity. Clones such as BGM 649, BGM 651, BGM 834 and BGM 876 had yields ranging between 3.2 to 5.7 dry t ha<sup>-1</sup> at 12 months, compared to 1.7 t ha<sup>-1</sup> of local checks. In semiarid environments such improved germplasm is crucial for food security where staple grain crops will probably fail to produce reasonable yields.

research, as that illustrated by the project conducted by CIAT and EMBRAPA/CNPMF, Brazil, on breeding improved cassava cultivars for the seasonally dry and semiarid environments, should not only be encouraged but also emulated in other crops. In view of the adverse effects on agricultural productivity in tropical countries that might result from observed global climate changes, more research on drought tolerance is warranted. Cassava, with its inherent capacity to tolerate and produce reasonably well under prolonged drought, should be expected to provide more essential food and feed than any other crop in marginal environments.

**Acknowledgement:** I am grateful for the sincere collaboration I received during the course of this research from the many workers, colleagues, associates, visiting scientists, students, secretaries at CIAT, and the Colombian farmers who generously offered logistic support and hospitality at their private farms and homes. The financial grants from The International Fund for Agricultural Development (IFAD), Rome, helped in initiating the collaborative breeding project between CIAT and the federal research organizations in Brazil

(EMBRAPA/CNPMF) in seasonally dry and semiarid areas of northeastern Brazil. Without this support, the achievements highlighted here would have never been realized. I am also thankful to my daughter, Farah El-Sharkawy Navarro, for her support in organizing the data in tables and figures and in searching the internet for needed information and references. The invaluable inputs provided by Dr. Mary Beth Kirkham, Kansas State University, Manhattan, Kansas, were also appreciated. The support from the editorial staff of BJPP in editing the original manuscript and in redrawing the many figures is also appreciated.

## REFERENCES

- Aguilar LP (1995) Ultraestructura foliar y fotosíntesis de yuca en diferentes cultivares (*Manihot esculenta* Crantz). Popayán, Universidad de Cauca. BSc thesis.
- Allem AC (2002) The origin and taxonomy of cassava. In: Hillocks RJ, Thresh JM, Bellotti AC (eds), Cassava: Biology, Production and Utilization, pp.1-16. CABI publishing, New York.
- Alves AAC (2002) Cassava botany and physiology. In:

- Hillocks RJ, Thresh JM, Bellotti AC (eds), Cassava: Biology, Production and Utilization, pp.67-89. CABI Publishing, New York.
- Augé RM, Schekel KA, Wample RL (1987) Leaf water and carbohydrate status of VA mycorrhizal rose exposed to drought stress. *Plant Soil* 99:291-302.
- Begonia GB, Begonia MT (2007) Plant photosynthetic production as controlled by leaf growth, phenology, and behavior. *Photosynthetica* 45:321-333.
- Berg VS, El-Sharkawy MA, Hernández A del P, Cock JH (1986) Leaf orientation and water relations in cassava. In: Annual Meeting of the American Society of Plant Physiologists, pp.186. Louisiana State University, Baton Rouge.
- Bernal LM (1991) Estudios sobre la actividad fosfoenolpiruvato carboxilasa en cultivares de yuca (*Manihot esculenta* Crantz). Bogota, Pontificia Universidad Javeriana. BSc. thesis.
- Blum A, Pnuel Y (1990) Physiological attributes associated with drought resistance of wheat cultivars in a Mediterranean environment. *Aust. J. Agric. Res.* 41:799-810.
- Blum A, Sullivan CY (1986) The comparative drought resistance of land races of sorghum and millet from dry and humid regions. *Ann. Bot.* 57:835-846.
- Bolaños J, Edmeades GO (1993a) Eight cycles of selection for drought tolerance in lowland tropical maize. I. Responses in grain yield, biomass, and radiation utilization. *Field Crops Res.* 31:233-251.
- Bolaños J, Edmeades GO (1993b) Eight cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. *Field Crops Res.* 31:253-268.
- Bolaños J, Edmeades GO, Martinez L (1993) Eight cycles of selection for drought tolerance in lowland tropical maize. III. Responses in drought-adaptive physiological and morphological traits. *Field Crops Res.* 31:269-286.
- Cadavid LF, El-Sharkawy MA, Acosta A, Sánchez T (1998) Long-term effects of mulch, fertilization and tillage on cassava grown on sandy soils in northern Colombia. *Field Crops Res.* 57:45-56.
- Caicedo JA (1993) Respuesta de cuatro cultivares de yuca (*Manihot esculenta* Crantz) a la modificación del estado hídrico del suelo. Palmira, Universidad Nacional de Colombia. BSc. thesis.
- Caldwell MM, Richards JH (1989) Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* 79:1-5.
- Cayón MG, El-Sharkawy MA, Cadavid LF (1997) Leaf gas exchange of cassava as affected by quality of planting material and water stress. *Photosynthetica* 34:409-418.
- CIAT (1987-1989) Cassava Program Annual Report for 1987-1989. Centro Internacional de Agricultura Tropical, Cali.
- CIAT (1992) Cassava Program Annual Report for 1992. Centro Internacional de Agricultura Tropical, Cali.
- CIAT (1993) Cassava Program Annual Report for 1993. Centro Internacional de Agricultura Tropical, Cali.
- CIAT (1995) Cassava Program Annual Report for 1995. Centro Internacional de Agricultura Tropical, Cali.
- Cock JH (1985) Cassava: New Potential for a Neglected Crop. Westview, Boulder.
- Cock JH, Franklin D, Sandoval G, Juri P (1979) The ideal cassava plant for maximum yield. *Crop Sci.* 19:271-279.
- Cock JH, Porto MCM, El-Sharkawy MA (1985) Water use efficiency of cassava. III. Influence of air humidity and water stress on gas exchange of field grown cassava. *Crop Sci.* 25:265-272.
- Cock JH, Riaño NM, El-Sharkawy MA, López F.Y, Bastidas G (1987) C<sub>3</sub>-C<sub>4</sub> intermediate photosynthetic characteristics of cassava (*Manihot esculenta* Crantz). II. Initial products of <sup>14</sup>C<sub>2</sub> fixation. *Photosynth. Res.* 12:237-241.
- Cohen JE (1997) Population, economics, environment and culture: an introduction to human carrying capacity. *J. Agric. Ecol.* 34:1325-1333.
- Connor DJ, Cock JH, Parra GE (1981) Response of cassava to water shortage. I. Growth and yield. *Field Crops Res.* 4:181-200.
- Connor DJ, Palta J (1981) Response of cassava to water shortage. III. Stomatal control and water status. *Field Crops Res.* 4:297-311.
- DaMatta FM, Ramalho JDC (2006) Impacts of drought and temperature stress on coffee physiology and production: a review. *Braz. J. Plant Physiol.* 18:55-81.
- Dawson TE (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95:565-574.
- de Tafur SM, El-Sharkawy MA, Cadavid LF (1997a) Response of cassava (*Manihot esculenta* Crantz) to water stress and fertilization. *Photosynthetica* 34:233-239.

- de Tafur MS, El-Sharkawy MA, Calle F (1997b) Photosynthesis and yield performance of cassava in seasonally dry and semiarid environments. *Photosynthetica* 33:249-257.
- Ellis JR, Larsen HJ, Boosalis MG (1985) Drought resistance of wheat plants inoculated with vesicular-arbuscular mycorrhizae. *Plant Soil* 86:369-378.
- El-Sharkawy MA (1990) Effect of humidity and wind on leaf conductance of field grown cassava. *Rev. Bras. Fisiol. Veg.* 2:17-22.
- El-Sharkawy MA (1993) Drought-tolerant cassava for Africa, Asia, and Latin America: breeding projects work to stabilize productivity without increasing pressures on limited natural resources. *BioScience* 43:441-451.
- El-Sharkawy MA (2004) Cassava biology and physiology. *Plant Mol. Biol.* 56:481-501.
- El-Sharkawy MA (2005) How can calibrated research-based models be improved for use as a tool in identifying genes controlling crop tolerance to environmental stresses in the era of genomics – from an experimentalists's perspective. *Photosynthetica* 43:161-176.
- El-Sharkawy MA (2006a) International research on cassava photosynthesis, productivity, eco-physiology, and responses to environmental stresses in the tropics. *Photosynthetica* 44:481-512.
- El-Sharkawy MA (2006b) Utility of basic research in plant/crop physiology in relation to crop improvement: a review and a personal account. *Braz. J. Plant Physiol.* 18:419-446.
- El-Sharkawy MA, Cadavid LF (2002) Response of cassava to prolonged water stress imposed at different stages of growth. *Exp. Agric.* 38:333-350.
- El-Sharkawy MA, Cadavid LF, de Tafur SM, Caicedo JA (1998) Genotypic differences in nutrient uptake and use efficiency of cassava as influenced by prolonged water stress. *Acta. Agron. Univ. Nacional-Palmira-Colombia* 48:9-22.
- El-Sharkawy MA, Cock JH (1984) Water use efficiency of cassava. I. Effects of humidity and water stress on stomatal conductance and gas exchange. *Crop Sci.* 24:497-502.
- El-Sharkawy MA, Cock JH (1986) The humidity factor in stomatal control and its effects on crop productivity. In: Marcelle R, Clijsters H, Van Poucke M (eds), *Biological Control of Photosynthesis*, pp.187-198. Martinus Nijhoff Publishers, Dordrecht.
- El-Sharkawy MA, Cock JH (1987a) C<sub>3</sub>-C<sub>4</sub> intermediate photosynthetic characteristics of cassava (*Manihot esculenta* Crantz). I. Gas exchange. *Photosynth. Res.* 12:219-235.
- El-Sharkawy MA, Cock JH (1987b) Response of cassava to water stress. *Plant Soil* 100:345-360.
- El-Sharkawy MA, Cock JH (1990) Photosynthesis of cassava (*Manihot esculenta*). *Exp. Agric.* 26:325-340.
- El-Sharkawy M, Hesketh J (1965) Photosynthesis among species in relation to characteristics of leaf anatomy and CO<sub>2</sub> diffusion resistances. *Crop Sci.* 5:517-521.
- El-Sharkawy MA, Hesketh JD (1986) Citation Classic-Photosynthesis among species in relation to characteristics of leaf anatomy and CO<sub>2</sub> diffusion resistances. *Curr. Cont. Agric. Biol. Environ.* 27:14. and <http://www.garfield.library.unpenn.edu/classics1986/A1986C891300001.pdf>
- El-Sharkawy MA, de Tafur SM (2007) Genotypic and within canopy variation in leaf carbon isotope discrimination and its relation to short-term leaf gas exchange characteristics in cassava grown under rain-fed conditions in the tropics. *Photosynthetica* 45:515-526.
- El-Sharkawy MA, Cock JH, Held KAA (1984) Water use efficiency of cassava. II. Differing sensitivity of stomata to air humidity in cassava and other warm-climate species. *Crop Sci.* 24:503-507.
- El-Sharkawy MA, Cock JH, Hernández A del P (1985) Stomatal response to air humidity and its relation to stomatal density in a wide range of warm climate species. *Photosynth. Res.* 7:137-149.
- El-Sharkawy MA, Cock JH, Porto MCM (1989) Características fotosintéticas da mandioca (*Manihot esculenta* Crantz). *Rev. Bras. Fisiol. Veg.* 1:143-154.
- El-Sharkawy MA, de Tafur SM, Cadavid LF (1992a) Potential photosynthesis of cassava as affected by growth conditions. *Crop Sci.* 32:1336-1342.
- El-Sharkawy MA, de Tafur SM, Cadavid LF (1993) Photosynthesis of cassava and its relation to crop productivity. *Photosynthetica* 28:431-438.
- El-Sharkawy MA, Hernández A del P, Hershey C (1992b) Yield stability of cassava during prolonged mid-season water stress. *Exp. Agric.* 28:165-174.
- El-Sharkawy MA, Hesketh JD, Muramoto H (1965) Leaf

- photosynthetic rates and other growth characteristics among 26 species of *Gossypium*. *Crop Sci.* 5:173-175.
- El-Sharkawy MA, Lopez Y, Bernal LM (2008) Genotypic variations in activities of phosphoenolpyruvate carboxylase and correlations with leaf photosynthetic characteristics and crop productivity of cassava grown in low-land seasonally-dry tropics. *Photosynthetica* 46 (in press).
- El-Sharkawy MA, Cock JH, Lynam JK, Hernández A del P, Cadavid LF (1990) Relationships between biomass, root-yield and single-leaf photosynthesis in field-grown cassava. *Field Crops Res.* 25:183-201.
- Evans LT, Wardlaw IF, King RW (1985) Plants and environment: two decades of research at the Canberra phytotron. *Bot. Rev.* 51:203-272.
- Evenson RE, Gollin D (2003) Assessing the impact of the Green Revolution, 1960 to 2000. *Science* 300:758-762.
- Fukuda WMG, Ender M, Iglesias C (1992-1993) Development of cassava germplasm for drier tropics and sub-tropical agro-ecosystems. Annual Report 1992-1993, Working Plan 1993-1994, CNPMF, EPAGRI, CIAT, Cruz das Almas, Brazil.
- Hall AE (2004) Breeding for adaptation to drought and heat in cowpea. *Eur. J. Agron.* 21:447-454.
- Hayman DS (1980) Mycorrhiza and crop production. *Nature* 287:487-488.
- Henry G, Hershey C (2002) Cassava in South America and the Caribbean. In: Hillocks RJ, Thresh JM, Bellotti AC (eds), *Cassava: Biology, Production, and Utilization*, pp.17-40. CABI Publishing, New York.
- Hernández ADP, Cock JH, El-Sharkawy MA (1989) The responses of leaf gas exchange and stomatal conductance to air humidity in shade-grown coffee, tea, cacao as compared with sunflower. *Rev. Bras. Fisiol. Veg.* 1:155-161.
- Hershey C, Jennings DL (1992) Progress in breeding cassava for adaptation to stress. *Plant Breed. Abstr.* 62:823-831.
- Howeler RH, Sieverding E (1983) Potentials and limitations of mycorrhizal inoculation illustrated by experiments with field grown cassava. *Plant Soil* 75:245-261.
- Hunt LA, Wholey WD, Cock JH (1977) Growth physiology of cassava. *Field Crops Abstr.* 30:77-91.
- Iglesias C, Brekelbaum T (1996) (eds) Proceedings of the 10<sup>th</sup> Symposium of the International Society of Tropical Root Crops. Centro Internacional de Agricultura Tropical, Cali.
- Iglesias C, Bonierbale M, El-Sharkawy M, Lozano L, Bellotti A, Wheatley C (1995) Focusing basic research for cassava varietal improvement. In: Howeler RH (ed), *Cassava Breeding, Agronomy Research and Technology Transfer in Asia*, pp.40-60. Centro Internacional de Agricultura Tropical, Cali.
- IPCC-Intergovernmental Panel on Climate Change (2006) IPCC Special Report on the Regional Impacts of Climate change – An Assessment of Vulnerability. UNEP, WMO. (<http://www.grida.no/climate/ipcc/regional/502.htm>).
- Jennings DL, Iglesias C (2002) Breeding for crop improvement. In: Hillocks RJ, Thresh JM, Bellotti AC (eds), *Cassava: Biology, Production, and Utilization*, pp.149-166. CABI Publishing, New York.
- Kamukondiwa W (1996) Alternative food crops to adapt to potential climatic change in southern Africa. *Clim. Res.* 6:153-155.
- Khalvati AM, Hu Y, Mozafar A, Schmidhalter U (2005) Quantification of water uptake by arbuscular mycorrhizal hyphae and its significance for leaf growth, water relations, and gas exchange of barley subjected to drought stress. *Plant Biol.* 7:706-712.
- Kirkham MB (1980) Efficiency of drought-resistant and drought-sensitive wheat cultivars in the use of elements in soil. *Phyton* 38:137-146.
- Kirkham MB (1988) Hydraulic resistance of two sorghums varying in drought resistance. *Plant Soil* 105:19-25.
- Kirkham MB, Suksayrettrup K, Wassom CE, Kanemasu ET (1984) Canopy temperature of drought-resistant and drought-sensitive genotypes of maize. *Maydica* 29:287-303.
- Kramer PJ (1980) The role of physiology in crop improvement. In: Staples RC, Kuhr RJ (eds), *Linking Research to Crop Production*, pp.51-62. Plenum Press, New York.
- Kramer PJ (1981) Carbon dioxide concentration, photosynthesis, and dry matter production. *BioScience* 31:29-33.
- Laetsch WM (1974) The C<sub>4</sub> syndrome: a structural analysis. *Annu. Rev. Plant Physiol.* 25:27-52.
- Lenis JJ, Calle F, Jaramillo G, Perez JC, Ceballos H, Cock JH (2006) Leaf retention and cassava productivity. *Field Crops Res.* 95:126-134.

- Levitt J (1980) Responses of Plants to Environmental Stresses, 2<sup>nd</sup> ed., Vol. 2. Academic Press, New York.
- Lokko Y, Anderson JV, Rudd S, Raji A, Horvath D, Mikel MA, Kim R, Liu L, Hernandez A, Dixon AGO, Ingelbrecht IL (2007) Characterization of an 18,166 EST dataset for cassava (*Manihot esculenta*) enriched for drought-responsive genes. *Plant Cell Rep.* 26:1605-1618.
- Long SP, Ainsworth EA, Leakey ADB, Nösberger J, Ort DR (2006) Food for thought: lower-than-expected crop yield stimulation with rising CO<sub>2</sub> concentration. *Science* 312:1918-1921.
- López Y, Veléz W, El-Sharkawy M, Meyer JE (1993) Biochemical characterization of PEPC from cassava: a preliminary report. In: Roca WM, Thro AM (eds), Proceedings of the First International Scientific Meeting of the Cassava Biotechnology Network, Cartagena, Colombia, pp.340-343. Centro Internacional de Agricultura Tropical, Cali.
- Ludlow MM, Muchow RC (1990) A critical evaluation of traits for improving crop yields in water-limited environments. *Adv. Agron.* 43:107-153.
- Madeley J (1994) Breeding for the tough spots: CGIAR researchers are developing crops that thrive in the harshest habitats. *CERES-The FAO Review.* Rome 26:22-26.
- Mooney HA, Gulmon SL, Rundel PW, Ehleringer JR (1980) Further observations on the water relations of *Prosopis tamarungo* of the northern Atacama desert. *Oecologia* 44:177-180.
- Nelsen CE, Safir GR (1982) Increased drought tolerance of mycorrhizal onion plants caused by improved phosphorus nutrition. *Planta* 154:407-413.
- Oguntunde PG (2005) Whole-plant water use and canopy conductance of cassava under limited available soil water and varying evaporative demand. *Plant Soil* 278:371-383.
- Oguntunde PG, Alatisé MO (2007) Environmental regulation and modelling of cassava canopy conductance under drying root-zone soil water. *Meteorol. Appl.* 14:245-252.
- Okogbenin E, Ekanyake IJ, Porto MCM (2003) Genotypic variability in adaptation responses of cassava to drought stress in the Sudan Savanna zone of Nigeria. *J. Agron. Crop Sci.* 189:376-389.
- Paul K, Yoh HH (1987)  $K_m$  values of ribulose-1,5-bisphosphate carboxylase of cassava cultivars. *Phytochemistry* 26:1965-1967.
- Pellet D, El-Sharkawy MA (1993) Cassava varietal response to phosphorus fertilization. I. Yield, biomass and gas exchange. *Field Crops Res.* 35:1-11.
- Pellet D, El-Sharkawy MA (1997) Cassava varietal response to fertilization: growth dynamics and implications for cropping sustainability. *Exp. Agric.* 33:353-365.
- Pinheiro HA, DaMatta MF, Chaves AR, Loureiro ME, Ducatti C (2005) Drought tolerance is associated with rooting depth and stomatal control of water use in clones of *Coffea canephora*. *Ann. Bot.* 96:101-108.
- Porto MCM (1983) Physiological mechanisms of drought tolerance in cassava (*Manihot esculenta* Crantz). Tucson, University of Arizona. PhD dissertation.
- Riaño MA, Cock JH, López Y, El-Sharkawy M (1987a) Anatomía Kranz, estructura y distribución de cloroplastos en hojas de yuca (*Manihot esculenta* Crantz). *Rev. Comalfi* 14:5-12.
- Riaño MA, Cock JH, López Y, El-Sharkawy M, Bastidas G (1987b) Características fotosintéticas de la yuca (*Manihot esculenta* Crantz): productos iniciales de fijación con <sup>14</sup>CO<sub>2</sub>. *Rev. Comalfi.* 14:13-17.
- Richards JH, Caldwell MM (1987) Hydraulic lift: Substantial nocturnal water transport between soil layers by *Artemisia tridentate* roots. *Oecologia* 73:486-489.
- Richards RA (2000) Selectable traits to increase crop photosynthesis and yield of grain crops. *J. Exp. Bot.* 51:447-458.
- Rosenzweig C, Parry ML (1994) Potential impact of climate change on world food supply. *Nature* 367:133-138.
- Safir GR (1985) Water relations and drought tolerance of vesicular-arbuscular mycorrhizal plants. In: Nuclear Techniques to Study the Role of Mycorrhiza in Increasing Food Crop Production. pp.127-132. International Atomic Energy Agency, Vienna.
- Sagrilo E, Filho PSV, Pequeno MG, Vidigal MCG, Scapim CA, Kvitschal MV, Maia RR, Rimoldi F (2006) Effect of harvest period on foliage production and dry matter distribution in five cassava cultivars during the second plant cycle. *Braz. Arch. Biol. Technol.* 49:1007-1018.
- Sasson A (1990) Feeding Tomorrow's World. United Nations Educational, Scientific and Cultural Organization (UNESCO)/CTA, Paris.

- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. Negative hydrostatic pressure can be measured in plants. *Science* 148:339-346.
- Setter TL, Fregene MA (2007) Recent advances in molecular breeding of cassava for improved drought stress tolerance. In: Jenks MA, Hasegawa PM, Jain SM (eds), *Advances in Molecular Breeding Toward Drought and Salt Tolerant Crops*, pp.701-711. Springer, Netherlands.
- Sieverding E, Howeler RH (1985) Influence of species of VA mycorrhizal fungi on cassava yield response to phosphorus fertilization. *Plant Soil* 88:213-222.
- Sieverding E, El-Sharkawy M, Hernandez AP, Toro T (1985) Influence of water stress on growth and formation of VA mycorrhiza of 20 cassava cultivars. In: *Mycorrhizae: Physiology and Genetics*, pp.717-720. INRA, Paris.
- Squeo FA, Olivares N, Olivares S, Pollastri A, Aguirre E, Aravena R, Jorquera C, Ehleringer JR (1999) Grupos funcionales en arbustos desérticos del norte de Chile, definidos sobre la base de las fuentes de agua utilizadas. *Gayana Bot.* 56:1-15.
- Turner NC (1986) Crop water deficits: a decade of progress. *Adv. Agron.* 39:1-51.
- Whan BR, Carlton GB, Siddique KHM, Regan KL, Turner NC, Anderson WK (1993) Integration of breeding and physiology: lessons from a water-limited environment. In: Buxton DR, Shibles R, Forsberg RA, Blad BL, Asay KH, Paylsen GM, Wilson RF (eds), *International Crop Science*, pp.607-614. Crop Science Society of America, Madison.
- Wortman S (1981) *Beyond the Bottom Line*. The Rockefeller Foundation, New York.