PHOTOSYNTHETICA 48 (2): 173-188, 2010

Comparative photosynthesis, growth, productivity, and nutrient use efficiency among tall- and short-stemmed rain-fed cassava cultivars

M.A. EL-SHARKAWY[*] and S.M. DE TAFUR[**]

Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia[*]
Universidad Nacional de Colombia, Sede Palmira, Colombia[**]

Abstract

Field trials under rain-fed conditions at the International Center for Tropical Agriculture (CIAT) in Colombia were conducted to study the comparative leaf photosynthesis, growth, yield, and nutrient use efficiency in two groups of cassava cultivars representing tall (large leaf canopy and shoot biomass) and short (small leaf canopy and shoot biomass) plant types. Using the standard plant density (10,000 plants ha^{-1}), tall cultivars produced higher shoot biomass, larger seasonal leaf area indices (LAIs) and greater final storage root yields than the short cultivars. At six months after planting, yields were similar in both plant types with the short ones tending to form and fill storage roots at a much earlier time in their growth stage. Root yield, shoot and total biomass in all cultivars were significantly correlated with seasonal average LAI. Short cultivars maintained lower than optimal LAI for yield. Seasonal P_N, across cultivars, was 12% greater in short types, with maximum values obtained in Brazilian genotypes. This difference in P_N was attributed to nonstomatal factors (*i.e.*, anatomical/biochemical mesophyll characteristics). Compared with tall cultivars, short ones had 14 to 24 % greater nutrient use efficiency (NUE) in terms of storage root production. The lesser NUE in tall plants was attributed mainly to more total nutrient uptake than in short cultivars. It was concluded that short-stemmed cultivars are superior in producing dry matter in their storage roots per unit nutrient absorbed, making them advantageous for soil fertility conservation while their yields approach those in tall types. It was recommended that breeding programs should focus on selection for more efficient short- to medium-stemmed genotypes since resource-limited cassava farmers rarely apply agrochemicals nor recycle residual parts of the crop back to the soil. Such improved short types were expected to surpass tall types in yields when grown at higher than standard plant population densities (>10,000 plants ha^{-1}) in order to maximize irradiance interception. Below a certain population density (<10,000 plants ha^{-1}), tall cultivars should be planted. Findings were discussed in relation to cultivation and cropping systems strategies for water and nutrient conservation and use efficiencies under stressful environments as well as under predicted water deficits in the tropics caused by trends in global climate change. Cassava is expected to play a major role in food and biofuel production due to its high photosynthetic capacity and its ability to conserve water as compared to major cereal grain crops. The interdisciplinary/interinstitutions research reported here, including an associated release of a drought-tolerant, short-stem cultivar that was eagerly accepted by cassava farmers, reflects well on the productivity of the CIAT international research in Cali, Colombia.

Additional keywords: agriculture; breeding, C_3-C_4; canopy; drought; ecophysiology; environment; gas exchange; leaf; *Manihot*; soils; tropics; yield.

Received 21 October 2009, *accepted* 7 February 2010.

[*] *Present address*: A. A. 26360, Cali, Valle, Colombia, e-mail: mabrouk99@hotmail.com; elsharkawy@emcali.net.co
[**] e-mail: smejiat@palmira.unal.edu.co

Abbreviations: C_3-C_4 species – photosynthetically intermediate species between typical C_3 and C_4 plants; DAP – days after planting; g_s – stomatal conductance; HI – harvest index; LAI – leaf area index; NUE – nutrient use efficiency; P_N – net photosynthetic rate; PEPC − phospho*enol*pyruvate carboxylase; PNUE – photosynthetic nitrogen use efficiency; Rubisco − ribulose-1,5-bisphosphate carboxylase/oxygenase.

Acknowledgements: We thank the many colleagues, workers, statisticians, and secretaries at CIAT whose collaboration was crucial during the course of the research. Articles reprints and courtesy copies of PhD theses received from many authors cited in the text were highly appreciated. We are indebted to Farah El-Sharkawy Navarro for her assistance in typing the manuscript and searching the internet for relevant information. We also thank the two anonymous reviewers and the editors of Photosynthetica for the many constructive comments on original version and for the additional materials incorporated into the revised text.

Introduction

Cassava (*Manihot esculenta* Crantz) is a staple food root-crop for more than 600 million inhabitants in the tropics and subtropics. It is cultivated as an annual and biennial crop for its starchy roots (approximately 85% starch on dry mass basis and less than 3% protein) that can be harvested at 8 to 18 months after planting (El-Sharkawy 1993, 2004). The roots are mainly consumed as human food in various forms after cooking and processing to remove the inherent cyanogenic glucosides, for animal feed, as well as for starch extractions and various industrial uses (Cock 1985, Splittstoesser and Tunya 1992, Alves 2002, El-Sharkawy 2004, Lebot 2009). World annual current production exceeds 214 million tons of fresh roots (about 50% occurs in sub-Saharan Africa), with an average yield of 10 t ha^{-1} (FAOSTAT 2007). In contrast with the capital-intensive 'Green Revolution' technology for dwarf/semi-dwarf cereal crops production which relies on application of agrochemicals and irrigation (Borlaug 1983), cassava is produced mainly by resource-limited small farmers on mostly marginal low-fertility acidic soils under rain-fed conditions (from less than 600 mm per year in semi-arid regions to over 1,500 mm in humid regions) without purchased agrochemical inputs (El-Sharkawy 1993, 2010). Although cassava is highly productive in favourable environments where more than 80 t ha^{-1} or less than 40 t ha^{-1} of fresh roots per 10–12 months are common in experimental trials and commercial fields with improved cultivars, respectively, its productivity in seasonally dry and semi-arid environments without fertilization is much less (Ramanujam 1990, El-Sharkawy 1993, 2004, 2010; El-Sharkawy *et al.* 1990, 1993; Pellet and El-Sharkawy 1993a, 1997; De Tafur *et al.* 1997a,b; De Tafur 2002, Fermont 2009, Fermont *et al.* 2009a,b). There is a large gap (more than six-fold) between yield potential and farmers yields, particularly in sub-Saharan Africa, due to lack of improved technologies (El-Sharkawy *et al.* 1990, El-Sharkawy 1993, Fermont 2009, Fermont *el al.* 2009b). Because of its inherent tolerance to prolonged drought and poor soils (El-Sharkawy 1993, 2006a, 2007), cassava production is expanding into more marginal lands and drier environments for subsistence (Romanoff and Lynam 1992, Fermont *et al.* 2008, 2009a,b). In sub-Saharan Africa, for example, cassava acreage increased from less than 6 million ha in 1961 to 12 million ha in 2007 and total production almost increased four-fold while yield increased from 6 t ha^{-1} to around 10 t ha^{-1} (FAOSTAT 2007). Nigeria is the world leader in cassava production with more than 34 million tons fresh root annually (FAOSTAT 2007). Moreover, its role is expected to be further strengthened because of its comparative advantages under drought and high temperature as compared, for example, to maize (Fermont 2009). With the observed rises in greenhouse gases that cause global climate change, cereal grain production in the tropics is predicted to decline (Rosenzweig and Parry 1994, IPCC 2006), thus, reducing dependence on crops like maize as main staple in most sub-Saharan African countries. In such scenarios, cassava cultivation for food, starch, animal feed, and for other industrial uses [*e.g.*, alcohol and biofuel (Jansson *et al.* 2009, Johnston *et al.* 2009)] would probably be further enhanced (Kamukondiwa 1996, Eke-Okoro *et al.* 2009). However, there are concerns about possible adverse environmental effects of increasing cassava cultivation in marginal lands without improved and more appropriate production technologies (Sarma and Kunchai 1991, Madeley 1994, El-Sharkawy 2006a, Ayoola and Makinde 2007, Fermont *et al.* 2008, 2009a).

The crop removes substantial amounts of nutrients from soils in both shoot and storage root biomass, particularly in high-productive ecosystems. However, with the exception of K, values are comparable with or even smaller (especially N, P, Mg) than values in cereal and grain legume crops per unit of harvested product (Cock 1985, Howeler 1991, 2002, Howeler and Cadavid 1983, 1990, Pellet and El-Sharkawy 1997, Ravi and Mohankumar 2004). In case of K, cassava removes per unit dry matter slightly more quantity than major cereal and legume crops because > 60% of K uptake is exported to harvested roots. In absence of fertilization on both clayey and sandy soils, continuous cassava cultivation for several years results in a decline in yield as well as in soil fertility (CIAT 1983–1998, Howeler and Cadavid 1990, Cadavid *et al.* 1998). Such a situation is further aggravated in hillside ecosystems where cassava is grown on steep marginal lands prone to water erosion that results in significant losses in organic matter and nutrients in absence of adequate cultural practices (Reining 1992, Zöbisch *et al.* 1995, Lal 1997, Ruppenthal *et al.* 1997). To minimize these environmental negative effects, improved technologies were sought for and developed *via* sound agronomic practices as well as genetic improvements (Leihner 1983, CIAT 1983–1998, Pellet and El-Sharkawy 1993a,b, 1997, Ernst-Schaeben 1994, Tscherning *et al.* 1995, Ruppenthal *et al.* 1997, Cadavid *et al.* 1998, El-Sharkawy *et al.* 1998a, El-Sharkawy and Cadavid 2000, Howeler 2002, El-Sharkawy 2004, Ravi and Mohankumar 2004). Planting grass barriers in hillside cassava-based systems reduced water runoff, soil erosion, and soil organic matter and nutrient losses, while maintaining and/or increasing cassava productivity (Ruppenthal *et al.* 1997, Leihner 2002). Introducing mulching with crop and weed residues also improved soil nutrients and water contents, enhanced soil organic carbon, decreased surface soil temperature, and increased cassava productivity, particularly in poor sandy soils (Cadavid *et al.* 1998, Howeler 2002). Working with several cassava cultivars grown in acidic Inceptisols in Colombia, Pellet and El-Sharkawy (1993b, 1997), El-Sharkawy *et al.* (1998a), and El-Sharkawy and Cadavid

(2000) found genetic diversity in nutrient use efficiency (NUE) in terms of storage root production per unit of nutrient uptake [kg(dry storage root) kg^{-1}(nutrient)]. In Kerala state, in southern India, Byju and Anand (2009) found that under sufficient rainfall (>1,500 mm in 10 months), the short duration improved cultivar, namely Sree Vijaya (6 months duration) had greater yield and greater NUE in terms of storage root production per unit of nitrogen uptake than the traditional cultivar, namely M-4 (10 month duration). Under prolonged water shortages imposed at different stages of cassava growth in the field, El-Sharkawy *et al*. (1998b) and El-Sharkawy and Cadavid (2002) found that NUE in terms of storage root production was significantly increased under early and mid-season water stress, as compared with well-watered crop with significant varietal differences. This phenomenon was attributed to the greater reduction in shoot biomass, relative to the reduction in storage roots, and consequently lesser total plant nutrient uptake. Furthermore, the reduction in shoot biomass, and not the reduction in leaf canopy which recovered rapidly after stress was ended, persisted after crop recovery from water stress after rainfall or irrigation; whereas root yield approached values in well-watered crop at final harvest. These important findings have led us to search for genetic variation in plant structure in relation to productivity and NUE which may enhance productivity in both fertile and poor soils (El-Sharkawy *et al*. 1998a). The approach of using genetic improvements based on plant phenotypic selection is of paramount importance since farmers don't normally recycle back to soils the residual top parts of cassava after harvest of storage roots and selection of planting materials from woody stems were made. Thus, large quantity of removed soil nutrients in above-ground plant parts is wasted (except when ashes from cassava dry stems used for household fuels are distributed back into the field, a practice followed by farmers in Kerala state, India). This paper deals with evaluating comparative leaf net photosynthetic rate (P_N) as measured in the field, crop growth, storage root yield, and NUE in a group of CIAT core germplasm that differ in their stem heights and leaf canopy.

Materials and methods

Plant materials and experimental design: A group of cultivars selected from CIAT core germplasm (Table 1) that differ in their stem heights with ranges from 2.3–2.6 m (denoted tall-stemmed) to 1.2–1.7 m (denoted short-stemmed), with associated differences in leaf canopy, were grown in two consecutive years (1994/1995, 1995/1996) at the CIAT Experimental station, at Santander de Quilichao, Cauca, Colombia (3°06' N;76°31'W, 990 m a. s. l., mean annual temperature 24°C). The soil at this experimental site is Inceptisol (FAO system) with clayey texture (about 71% clay, 25% silt, and 4% sand). Soil chemical characteristics were pH (water) of 4.5, an organic carbon content of 2.8 mol C kg^{-1}(dry soil), and mineral contents of 0.41 NH_4, 0.18 NO_3, 0.40 P, 1.80 K, 9.50 Ca, 3.70 Mg, and 9.59 Al mmol kg^{-1}(dry soil).

A split-plot (the size of a sub-plot was 60 m^2) design was used with four replications. The main plots were assigned to groups of plant structure (*i.e.*, tall- and short-stemmed) and the sub-plots to cultivars within each group. Mature stem cuttings, 0.20 m, were pretreated by soaking for 10 min in a fungicide-insecticide zinc-sulfate solution before planting. On October 4th 1994, and September 28th 1995, the cuttings were planted vertically on ridges 1 × 1 m to give 10,000 plants ha^{-1} (the standard cropping practice). However, this population density favoured tall cultivars over short ones due to higher top biomass and greater leaf canopy in the former. One month after planting in both years, 50 N, 44 P, 84 K kg ha^{-1} in the form of 10:8.7:16.7 NPK compound fertilizer were band-applied near the sprouting plants (at this growth stage few leaves had appeared).

The trials received 1,461 mm and 1,927 mm of rainfall during 1994/1995 and 1995/1996, respectively. These quantities of rainfall exceeded pan evaporation rates of 4.4 mm d^{-1} at this site. No irrigation was applied in either growing season. However, the distribution patterns of the precipitation were uneven in both years with two marked dry periods, *i.e.*, end of December to middle of March, and from July to middle of September. During two months before harvests in both years, there were severe water deficits. In the first growing season, there was a prolonged drought period from 110 to 170 days after planting (DAP).

Biomass, storage root yield, and nutrient uptake determination: Four sequential harvests in both years of 6 protected plants were made per sub-plot at 2, 4, 6, and 10 months after planting. Plants were separated into leaves, petioles, stems, and storage roots, and samples from each part were chopped and oven-dried at 75°C until constant mass was obtained. Properly grounded dry subsamples were digested in sulfuric acid and the contents of N and P in solution were determined colorimetrically on an auto-analyzer; K, Ca, and Mg were determined by atomic absorption spectrometry. The nutrient uptake in harvested samples (except fallen leaves that were not collected in this case) was calculated per unit of total dry mass and then converted into kg ha^{-1}. NUE in terms of storage root production was determined in both years.

Leaf area index (LAI) and leaf P_N measurements in tall and short cassava: LAI was determined (non-destructively) periodically starting from day 45 DAP to 280 DAP using *LAI-2000* Plant Canopy Analyzer (*LICOR*, Lincoln, Nebraska, USA) that computed time-integrated LAI from radiation interception. The radiation interception was measured from five locations within each sub-plot between 09:00–11:00 local time. In the short-stemmed cultivars, radiation interception was always lower than values measured with tall-stemmed cultivars because of lower LAI in the former. Under the population density (10,000 plant ha^{-1}) used in these trials, short-stemmed cultivars lacked complete canopy closure in most of the growing season.

Leaf P_N was determined periodically with an *LCA-2* portable system (*Analytical Development Co.,* Hoddesdon, England), which consisted of an air pump, infrared gas analyzer (IRGA), data logger, and Parkinson Broad Leaf Model chamber. The P_N was measured on mature upper canopy leaves using atmospheric air [345 µmol (CO$_2$) mol^{-1}(air)] drawn from above canopy using a vertically mounted 4-m glass-fiber probe connected to a pump. All measurements were made under a solar irradiance higher than 1,200 µmol m^{-2} s^{-1} (of photosynthetically active radiation) between 8:00–12:00 local time. The leaf chamber was clamped over the middle portion (6.25 cm^2 surface area) of the central lobe of the measured leaves, and was held toward the sun for 30 to 60 s to obtain steady-state gas exchange rates (both CO$_2$ uptake and H$_2$O loss). Air temperature in the cuvette varied between 28 and 33°C, depending on time and date of measurement. It is noteworthy that this temperature range is within the optimal thermal range for photosynthesis and growth of cassava. Measurements were always made in low-rainfall periods that sometimes spanned several weeks. Four leaves (one leaf per sub-plot) were measured for each cultivar. On rainy days (high air humidity and wet soils) the few maximum P_N values were measured and ranged from 35 to over 40 µmol(CO$_2$) m^{-2} s^{-1}. Seasonal average P_N was calculated from all measurements recorded between 45 DAP to 180 DAP.

Results and discussion

Comparative LAI dynamics over time, and shoot and storage root biomass: Figs. 1 and 2 illustrate dynamics of leaf canopy formation during the first growing season in individual cultivars in the two plant types [data from the second season (not shown) showed similar responses]. In all cultivars in both plant types, LAI progressively increased from the initial measurement date (45 DAP) reaching a peak at 3–4 months after planting, then declined during a low-rainfall period. A second peak during high rainfall was observed at 6–7 months in most cultivars. This trend in LAI of cassava in sub-humid areas with two peaks of rainfall is common (Cock 1985, Veltkamp 1985, El-Sharkawy and Cock 1987b, El-Sharkawy *et al* 1992b, Pellet and El-Sharkawy 1997, De Tafur *et al.* 1997a, El-Sharkawy and Cadavid 2002). Cultivar differences in LAI within each plant type were significant. The tall cultivars had larger LAI than the short ones as shown by the across cultivar averages (seasonal mean LAI values were 2.56 and 1.72 for tall and short types, respectively) (Fig. 3). Moreover, there was a steeper decline in LAI in short cultivars from 200 to 280 DAP (about 40% reduction) in contrast with trends in tall cultivars (about 27% reduction) (Fig. 3).

The smaller seasonal mean LAI in short cultivars, as compared to tall ones, was a limiting factor for light interception at a population density of 10,000 plants ha^{-1}, and consequently, total biomass accumulation (storage roots and shoots) in this group was significantly lower as compared to tall cultivars (Table 1, Fig. 4). However, much of the reduction in total biomass in short types was attributed to a much smaller shoot biomass rather than storage roots biomass, resulting in higher harvest index (HI = storage root dry mass/total biomass) (Table 1). Furthermore, shoot growth in tall cultivars continued to increase sharply until the final harvest, while in short ones much smaller increases in shoot biomass occurred between 4 and 10 months, indicating the priority to divert more photoassimilates to storage roots (compare data in Fig. 4). This inherent trend in short cultivars points to their potential to maximize storage root yield in a shorter time and provides an opportunity to select for earliness and short duration genotypes that could be targeted to drier tropical environments with short rainy periods such as northeastern Brazil, and western coasts of Ecuador and Peru. In Africa, Asia and Latin America, where cassava production is often intercropped with cereals and grain legumes (Leihner 1983, CIAT 1983-1998, Ernst-Schaeben 1994, Ravi and Mohankumar 2004), short-stemmed cultivars would be advantageous and more adaptable in this case. In general, intercropping cassava with cereals or grain legumes is beneficial in reducing risks of crop failure in drier years where cereals and legumes suffer the most from water deficits, increasing profitability per unit land, reducing pest incidence, and diminishing soil erosion in hillside ecosystems (Francis 1986, Altieri and Liebman 1986, Ruppenthal *et al.* 1997, Iijima *et al.* 2004).

In single-cropping systems, and at plant population densities greater than 10,000 plants ha^{-1}, short-stemmed cassava cultivars are expected to possess larger LAI and yield more since root yield and shoot biomass were strongly related to seasonal mean LAI (Fig. 5). Cock *et al.* (1979), El-Sharkawy and Cock (1987b), and Cock and El-Sharkawy (1988) have illustrated *via* simulation modeling and experimental data that storage root yield increases with average seasonal LAI up to values between 2.0 to 3.5 and then tends to decline with further increases in LAI since shoot biomass strongly competes for photoassimilates at larger LAI. This optimal response is substantiated by the decreasing trend in HI with increased LAI above an optimum value observed in these cultivars (Fig. 6, Table 1, $r = -0.571$, $p<0.05$). The

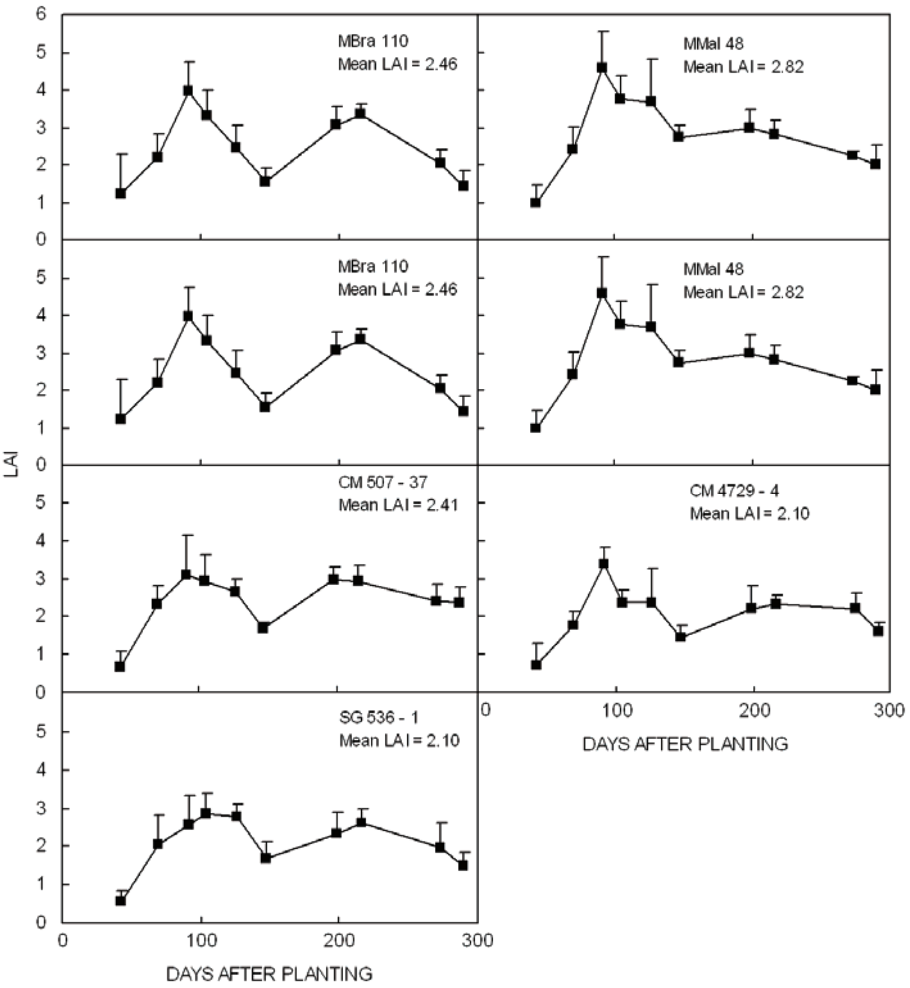

Fig. 1. Dynamics of leaf area index (LAI) as a function of time after planting of individual tall cultivars during the first growing season. Data points are means ± SD (four measurements from separate sub-plots).

apparent reason for this pattern is that the cassava ‘nodal unit’ (which consists of a node, a bud, a palmate leaf blade subtended by a long petiole, and an internode whose length and mass depend on the genotype) has a larger mass in most early-branching tall, and vigorous genotypes with thick stems such as M Mex 59 (El-Sharkawy 2004). However, there are exceptions with leafy cultivars possessing thinner stems and shorter internodes [with less dry mass allocated to their ‘nodal unit’ while retaining large leaf area (greater leaf area ratio, *i.e.*, larger leaf area per unit mass of shoot as was observed in the short-stemmed type with about 5.44 m^2 kg^{-1} in contrast with about 4.2 in tall-stemmed ones)], where the optimum seasonal LAI could reach higher values (El-Sharkawy *et al.* 1992b). In these two groups of plant types, tall cultivars reached the postulated range of optimal seasonal mean LAI (2.56) expected for maximum storage root yield, whereas the short ones had much lower LAI values (1.70), and thus, lower final yields.

The short types appear to have earlier storage root formation and filling than the tall ones (at 4-month after planting, short cultivars had 2.10 t ha^{-1} oven-dried storage roots averaged for both years, as compared to 1.35 t ha^{-1} in tall ones, and maintained equal yields with tall cultivars up to 6 months after planting). When combined with long leaf life [*i.e.*, better leaf retention, (El-Sharkawy *et al.* 1992b, Lenis *et al.* 2006, Orek *et al.* 2008, Zhang *et al.* 2010)], high dry matter contents in storage roots, early bulking, and tolerance to pests and diseases (Hillocks *et al.* 2002), short-stemmed cultivars with shorter growth cycle (< 10 months) might be advantageous in ecozones with short rainfall season (less than 7 months and < 700 mm rainfall) as in some seasonally dry and semiarid regions in the tropics [for example, in northeastern Brazil, (El-Sharkawy 1993, 2007, 2010)]. In this case, agronomic practices that ensure better weed control and conservation of soil water [*e.g.*, increased plant population densities and use of surface plant mulch (Cadavid *et al.* 1998, Sangakkara *et al.* 2004)] would further enhance cassava productivity. Increasing plant population densities in short-stemmed cultivars would ensure greater LAI and light interception

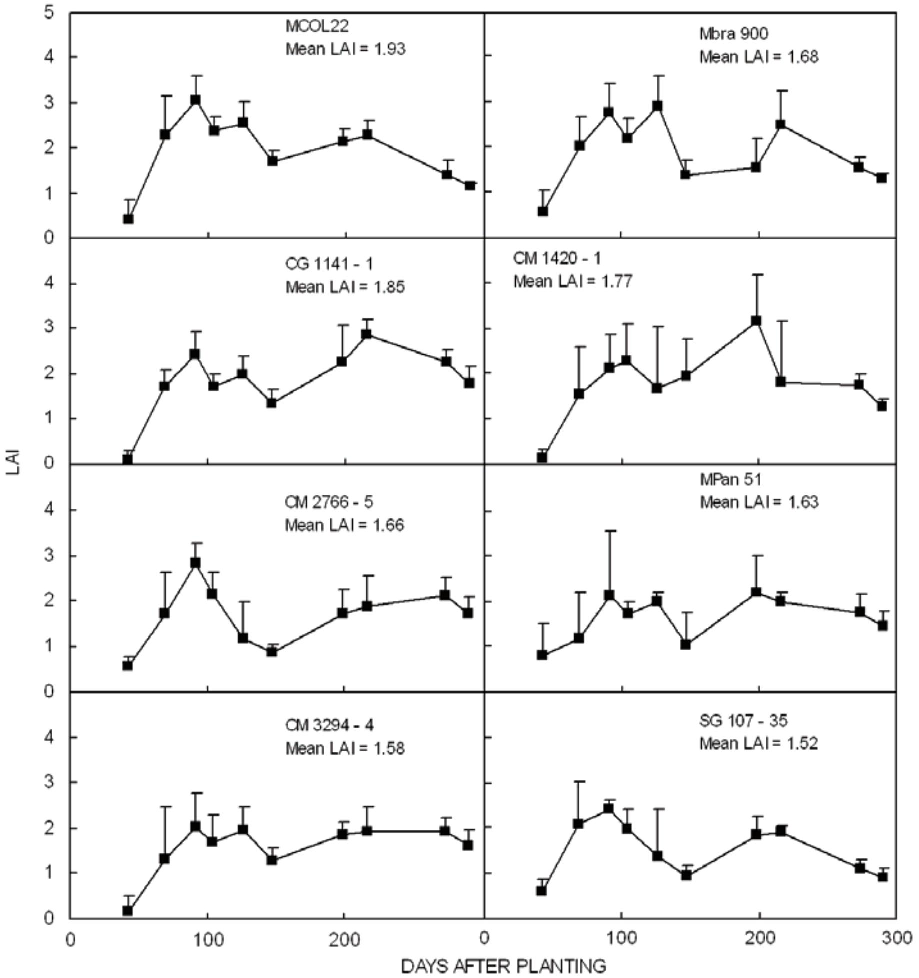

Fig. 2. Dynamics of of leaf area index (LAI) as a function of time after planting of short individual cultivars during the first growing season. Data points are means ± SD (four measurements from separate sub-plots).

during most of the growth cycle and, thus, higher yields (Fig. 5). Applying surface plant mulch reduces weed competition with the crop for both nutrients and water, mitigates water evaporation from exposed soil when canopy is not fully closed during the growth cycle, diminishes surface soil temperature, and as well reduces the frequency and needs for weeding (Cadavid *et al.* 1998, Sinkevičienė *et al.* 2009). In absence of fertilization on sandy low-fertility soils, long-term mulching enhanced leaf canopy, storage root yield, soil organic carbon, soil nutrient contents, and reduced cyanogenic glucosides in storage root parenchyma (Cadavid *et al.* 1998), hence, improving root quality for human consumption (Essers 1995).

Cassava stomata exert tight control on transpirational water losses in dry hot air and with soil water deficits, while leaves remain fixing substantial CO_2 amounts (*e.g.* 40–60% of rates under nonlimiting soil water and high air humidity) (Connor and Palta 1981, Porto 1983, El-Sharkawy and Cock 1984, 1986; Cock *et al.* 1985, El-Sharkawy 1990, 1993, 2006a; De Tafur 2002, De Tafur *et al.* 1997a,b; Oguntunde 2005, Oguntunde and Alatise 2007). This characteristic underlies cassava tolerance to prolonged drought where most cereal and grain legumes crops would probably fail. Coupled with stomatal characteristics, deep rooting traits must be bred for to take advantage of available deep wet soil layers (El-Sharkawy 2007, 2010). Leaf retention is essential in short-stemmed cultivars to maximize light interception. This trait seems to be related with fine rooting systems, and hence, could be used as an indirect morphological indicator for screening large germplasm accessions under prolonged water deficits conditions (El-Sharkawy and Cock 1987b, El-Sharkawy *et al.* 1992b, Lenis *et al.* 2006).

Because cassava is a vegetative propagated plant, conventional breeding methods, based mainly on controlled and/or open crossing schemes among heterozygous parental materials followed by several cycles of field evaluation among F1 populations, require 10–15 years for selecting improved clones (Hershey and Jennings 1992, Kawano 2003). Alternatively, molecular marker assisted selection approaches were advocated, particularly for

Table 1. Comparative seasonal upper canopy leaf photosynthetic rate (P_N), seasonal stomatal conductance (g_s), seasonal leaf area index (LAI), final (10 months) storage root yield, shoot and total biomass, and harvest index (HI) for tall- and short-stemmed cassava cultivars. Data of storage root yield, shoot and total biomass are means of two growing seasons.* Note the high seasonal P_N in Brazilian genotypes, MBra 110 and MBra 900, as compared to values of other cultivars within tall- and short-stemmed groups, respectively. Brazil-originated cassava germplasm was included as genetic source for crop improvement at CIAT breeding program for decades. Also, the high yielding MMal 48 was later introduced from Malaysia. Several CIAT improved clones showed high yields as well, particularly within short-stemmed group. NS – not significant at 0.05.

Cultivar	LAI	Seasonal P_N [μmol(CO$_2$) m^{-2} s^{-1}]	Seasonal g_s [mol m^{-2} s^{-1}]	Final dry root yield [t ha^{-1}]	Final dry shoot biomass [t ha^{-1}]	Final total biomass [t ha^{-1}]	HI
Tall – high LAI							
CG 402 - 11	3.13	15.68	1.3	11.9	8.0	19.9	0.60
CM 4574 - 7	2.91	14.45	1.4	14.5	5.8	20.3	0.71
MBra 110*	2.46	17.18	1.6	11.4	7.6	19.0	0.60
MMal 48	2.82	15.89	1.6	17.2	7.3	24.5	0.70
CM 507 - 37	2.41	15.61	1.4	12.4	4.7	17.1	0.73
CM 4729 - 4	2.10	17.16	1.6	13.0	5.5	18.5	0.70
SG 536 - 1	2.10	16.58	1.5	9.2	3.7	12.9	0.71
Mean	2.56	16.08	1.5	12.8	6.09	18.89	0.68
Short – low LAI							
MCol 22	1.93	17.54	1.5	8.5	2.5	11.0	0.77
MBra 900*	1.86	21.44	1.7	8.5	2.7	11.2	0.76
CG 1141 - 1	1.85	17.23	1.5	12.7	2.4	15.1	0.84
CG 1420 - 1	1.77	17.93	1.5	9.0	2.2	11.2	0.80
CM 2766 - 5	1.66	15.59	1.5	10.1	3.2	13.3	0.76
MPan 51	1.63	17.86	1.3	8.7	4.9	13.6	0.64
CM 3294 - 4	1.58	18.38	1.5	10.4	3.3	13.7	0.76
SG 107 - 35	1.51	18.18	1.2	11.2	4.1	15.3	0.73
Mean	1.72	18.02	1.5	9.89	3.16	13.05	0.76
LSD 5% between groups means	0.4	1.75	NS	1.9	1.1	2.8	0.06

simple-inherited traits, to shorten evaluation time as well as to enhance selection efficiency (Setter and Fregene 2007). Moreover, the use of gene manipulating/transgenic biotechnology coupled with development of molecular markers to facilitate the introgression into cassava cultivars gene(s) controlling 'exotic' and specific drought-tolerance related traits such as 'staygreen' was recently suggested by (Orek *et al.* 2008, Zhang *et al.* 2010) which may accelerate identifying genes controlling leaf retention and fine root systems in short-stemmed genotypes. Since production of transgenic plants in large numbers is difficult, laborious, and commercially expensive, transgenes should be inserted into already agronomically improved cultivars *via* conventional breeding (Visarada *et al.* 2009). Thus, the combination of 'specific-gene' introgression and 'phenotypic-based' trait selection might be the right breeding approach for improving productivity and tolerance to drought (Salekdeh *et al.* 2009).

A good example of the transgenic approach is the recent achievement and identification of genes that possibly control photoperiodism and flowering in cassava (Adeyemo 2009). These findings have important implications for cultivars where flowering is scarce or absent, which complicates their use in breeding programs. Moreover, enhancing flowering, and consequently seed production, may facilitate shifting from vegetative to sexual propagation system, and hence, obviate the many biotic constraints associated with the former system (*e.g.* Iglesias *et al.* 1994). Unfortunately, the lack of communication/cooperation between plant physiologists, breeders, and molecular biologists has hindered progress in crop improvement in most national programs. As cassava producers are faced with the necessity to achieve sustainable crop yields under the many environmental stresses and global climate change conditions, as well as an ever-growing human population, such cooperation becomes mandatory. International organisations involved with agricultural research and development must take a major role in filling this gap, particularly by conducting the essential basic research which is unaffordable, but required, by developing countries. El-Sharkawy (2005, 2006b) reviewed the role of basic physiological research in crop improvement and highlighted the many contributions that such research had achieved in the past decades. At CIAT, the basic physiological research was pivotal in strengthening the cassava breeding and improvement program (Iglesias *et al.* 1995).

A short-stemmed cultivar M Col 2215, endowed with high dry matter contents in its roots (> 400 g kg^{-1}), stable yield, high level of tolerance to drought, high HI (>0.70) and better leaf retention was selected from 1987–1989 trials in the seasonally dry Patía Valley, Cauca, Colombia, (El-Sharkawy *et al.* 1990) and later tested in the semi-arid ecozone of the west Coast of Ecuador (< 600 mm rainfall with long dry period). Local farmers participated in field trials evaluation across years and locations and quickly multiplied their planting material, which indicates high acceptance and adoption of short plant types. It was officially released in August 1992 under the name Portoviejo 650 by the Instituto Nacional de Investigación Agropecuaria (INIAP), Portoviejo, Manabi Province, Ecuador (CIAT 1993, El-Sharkawy *et al.* 2008). It is noteworthy here to emphasize the collaborative efforts of two former CIAT scientists, the breeder E.E. Carey (CIP, Peru), who provided the initial 127 cassava accessions, and the sociologist S. Romanoff (Rockefeller Foundation, USA), who co-ordinated the cassava technology transfer in Ecuador.

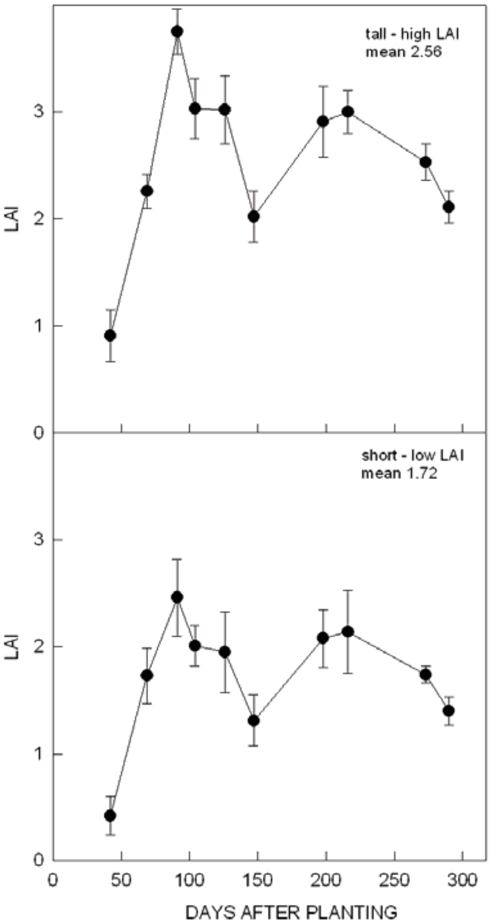

Fig. 3. Across all cultivars average leaf area index (LAI) [m^2(one-side leaf surface) m^{-2}(land surface)] in tall and short types in the first growing season as a function of time. Data points are means ± SD (n = 28 for tall-stemmed cultivars and 32 for short-stemmed cultivars). Note: (a) the drop in mean LAI between 110–150 DAP due to a prolonged drought; (b) the steeper decline in LAI in short cultivars from 200 to 280 DAP (about 40% reduction) in contrast with trends in tall cultivars (about 27% reduction).

Comparative P_N in tall and short cassava: Figs. 7 and 8 illustrate P_N (in upper canopy leaves) as measured during the first growing season in tall and short cultivars. The rates varied with time of measurements and cultivars. As the season progressed, there was a declining pattern in leaf photosynthetic rates in all cultivars with the lowest values corresponding to a long dry period that extended between 110 and 170 DAP (Fig. 9). In these trials, seasonal average rates were much lower than the maximum P_N obtained in rainy days [>30 μmol(CO_2) m^{-2} s^{-1}, (Fig. 8) and cultivar MBra 900]. El-Sharkawy *et al.* (1992a, 1993) and El-Sharkawy and De Tafur (2007) reported seasonal average P_N that varied from 26 to

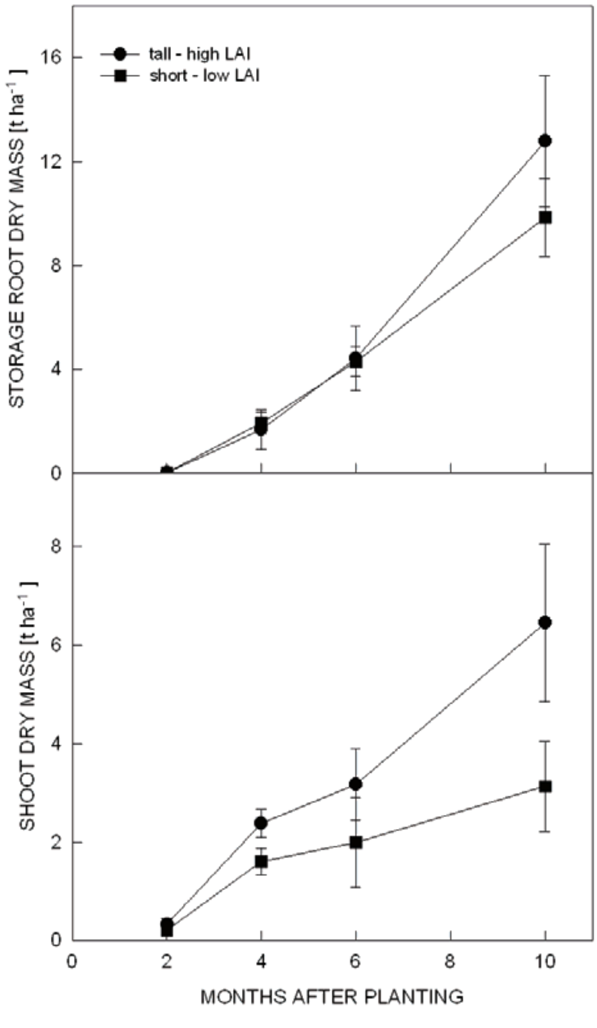

Fig. 4. Shoot dry biomass (stems plus attached leaves) (*lower panel*) and storage root dry mass (*upper panel*) at different harvest dates. Data points are grand means ± SD of two years (8 replications for each cultivar) for 8 short-stemmed and 7 tall-stemmed cultivars.

36 μmol(CO_2) m^{-2} s^{-1} in 15 cultivars grown under rain-fed conditions at the same site of the present trials, with the highest rates observed in Brazilian cultivars such as MBra 191 and MBra 12. Maximum upper canopy $P_N >$ 45 μmol(CO_2) m^{-2} s^{-1} was recorded in MBra 191 during the rainy period (El-Sharkawy *et al.* 1992a). From these findings, it appears that genetic diversity in photosynthetic capacity could be traced and related to original habitats from which CIAT cassava germplasm was obtained. Large portion of Brazilian germplasm originated in hot-humid environments where cultivated cassava is thought to be domesticated and where a possible wild ancestor/progenitor [*M. esculenta* ssp. *flabellfolia* (Pohl) Cifferi] was recently reported in the central Brazilian state of Goiás (Allem 2002). Morphological, biochemical and molecular characteristics were found to lend support to Allem's hypothesis on cassava Brazilian geographical and botanical origin. Thus, the high photosynthetic potential observed in Brazilian cultivars in the present trials and in previous reports may also support Allem's hypothesis. Furthermore, the rapid closure of cassava stomata in dry air irrespective of soil water conditions and bulk leaf water potential (El-Sharkawy and Cock 1984) might be taken as another physiological evidence that cassava originated in hot-humid environments, probably in Amazonia, as suggested by Allem (2002). Moreover, in comparative structural and photosynthetic studies between cultivated cassava and its postulated wild ancestor (*M. esculenta* ssp. *flabellfolia* (Pohl) Cifferi), Pujol *et al.* (2008) reported higher P_N in cassava with increasing differences when rates were expressed on leaf mass rather than on leaf area basis (*i.e.*, cassava has thinner leaves than its wild ancestor). These authors suggested that domestication probably entailed resource-acquisition strategy (*i.e.*, cassava evolution and domestication took place in habitats rich in edaphic resources and under high irradiances), which led to greater photosynthetic rate and specific leaf area (*i.e.*, leaf area per unit mass) in domesticated cassava.

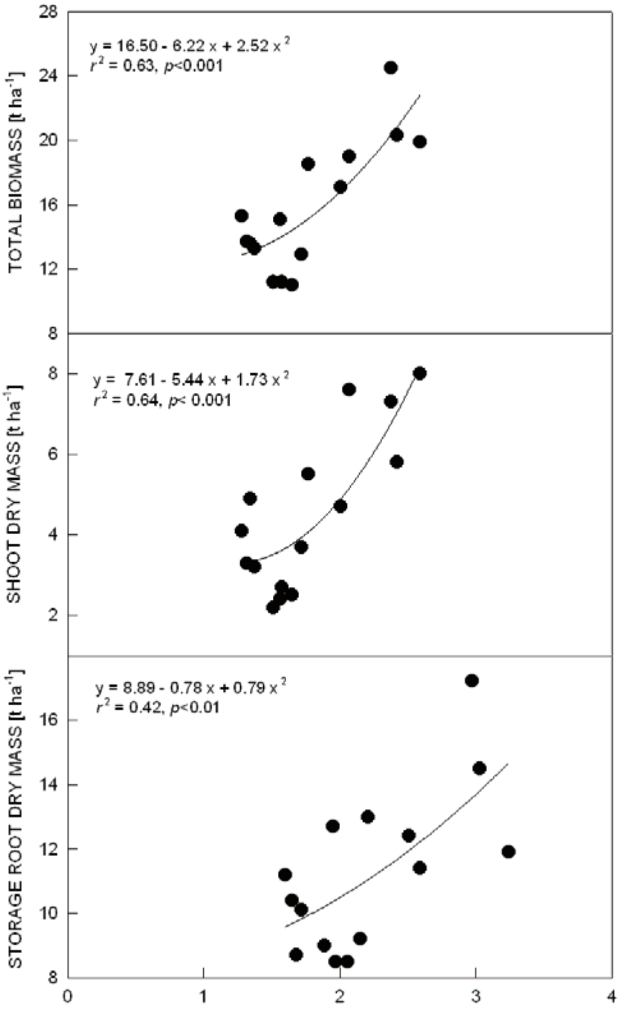

Fig. 5. Relationships between seasonal mean leaf area index (LAI) [m^2(one-side leaf surface) m^{-2}(land surface)] and storage root yield, shoot and total biomass (excluding fallen leaves) for tall- and short-stemmed cultivars. Data points represent individual cultivars and are means of eight replications for storage roots, shoots and total biomass and 40 determinations of LAI. Note the stronger correlations between seasonal LAI and total and shoot biomass as compared with value in storage root.

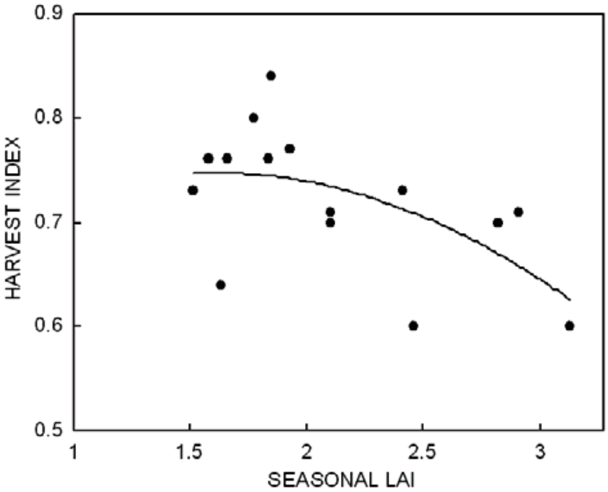

Fig. 6. Relationship between seasonal leaf area index (LAI) [m^2(one-side leaf surface) m^{-2}(land surface)] and harvest index (HI) (storage root dry mass/total biomass excluding fallen leaves) across combined tall- and short-stemmed cultivars ($y = 0.611 + 0.168\,x - 0.052\,x^2$, $r^2 = 0.326$, $p<0.05$). Data points represent individual cultivars and are means of 8 replications for HI and 40 determinations for LAI.

As a group, short-stemmed cassava cultivars appeared to maintain higher seasonal P_N, as compared to tall ones (on average, about 12% greater P_N than values in tall cultivars, Fig. 9 and Table 1). The higher seasonal P_N in short cassava cultivars might partly explain why their final root yield approached that in tall ones despite their

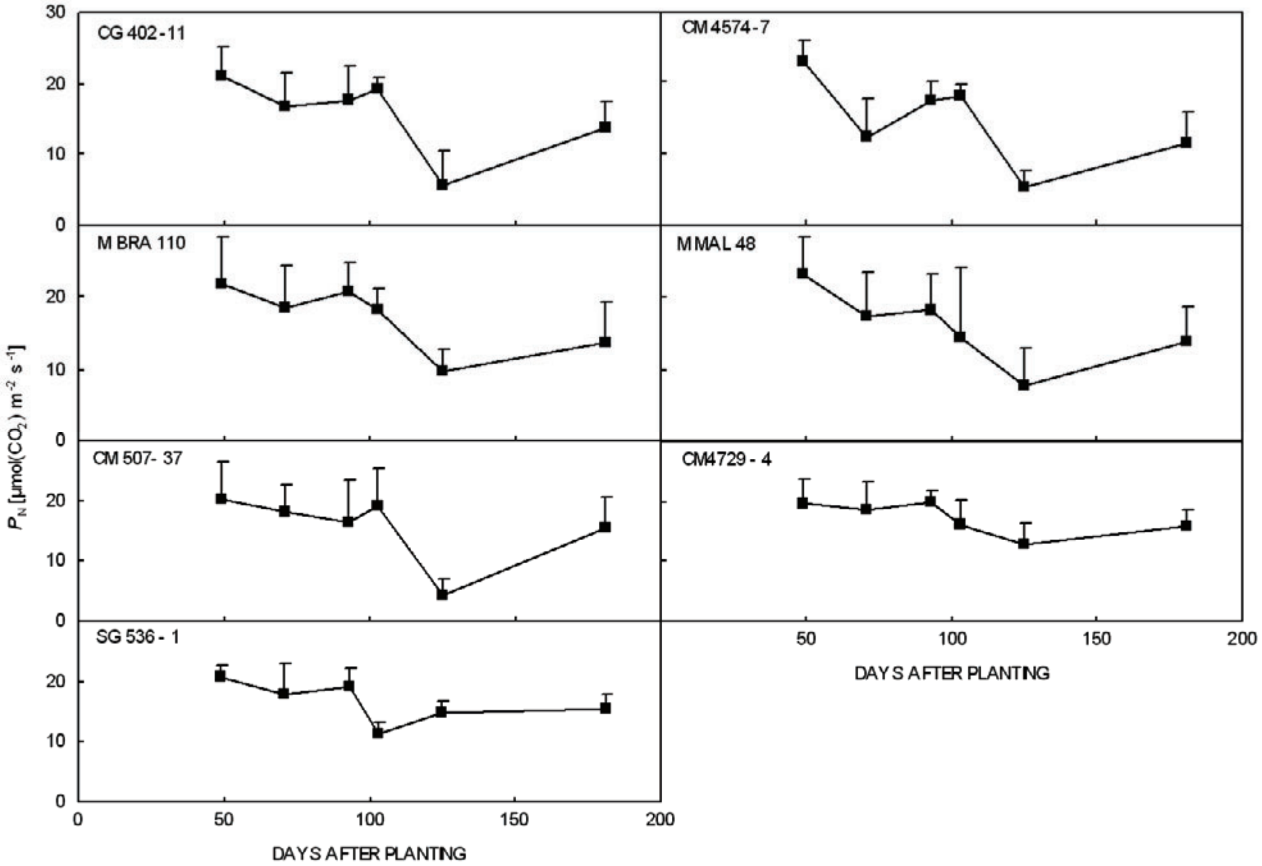

Fig. 7. Upper canopy leaf photosynthetic rate (P_N) of individual tall cultivars. Data points are means ± SD ($n = 4$). Note the high maximum P_N in MBra 110 and MMal 48 and the lesser drop during the prolonged drought between 110–150 DAP, as compared to other cultivars.

much smaller LAI (Figs. 3,4). Stomatal conductance to gas exchange (Table 1) was not significantly different among the two plant types, which might indicate that differences in P_N were probably caused by nonstomatal factors (*i.e.*, leaf anatomical/biochemical characteristics). It is known that significant variations in activities of photosynthetic enzymes such as the C_3 ribulose-1,5-bisphosphate craboxylase-oxygenase (Rubisco) and the C_4 phospho*enol*pyruvate carboxylase (PEPC) exist in cassava germplasm (El-Sharkawy 2004, 2006). Thus, differences among plant type photosynthetic rates might be due to differences in enzyme activities and/or contents of enzymes proteins in leaf mesophyll tissues. It is possible that short-stemmed cultivars with small leaf canopy, as indicated by their low values of seasonal LAI (Table 1, Fig. 3), might possess concentrated photosynthetic machinery in its leaves, as compared with the larger leaf canopy in tall cultivars. This characteristic is important since photosynthetic nitrogen use efficiency (PNUE) (CO_2 uptake per unit leaf total nitrogen) was found to be positively correlated with upper canopy P_N, with C_4 PEPC activities, and as well with storage root yield in large and phenologically/morphologically diverse germplasm grown in different environments (El-Sharkawy 2004, El-Sharkawy *et al*. 2008). High PNUE in cassava may underly the reasonable yields obtained in cassava grown continuously without fertilization (8–10 years) on both clayey acidic and sandy soils with low fertility in Colombia (CIAT 1983–1998, Howeler 1991, Cadavid *et al.* 1998).

Differences among cultivars in seasonal P_N are apparent in both plant types. The highest rates were observed in MBra 110 and MBra 900 within tall and short types, respectively (Table 1). Furthermore, MBra 900 had the highest maximum leaf photosynthetic rate [$P_N > 30$ μmol(CO$_2$) m^{-2} s^{-1}, Fig. 8] as well as the greatest seasonal P_N [21.44 μmol(CO$_2$) m^{-2} s^{-1}, Table 1] among the two sets of cultivars. These findings further substantiate the high photosynthetic potential in Brazil-originated germplasm. The cassava breeding program at CIAT took advantage of the promising potential of Brazilian germplasm and included several cultivars and landraces as genetic sources to strengthen the cassava genetic base for crop improvement, particularly under stressful environments (Hershey and Jennings 1992, Fukuda *et al.* 1992–1993, El-Sharkawy 1993, 2007, 2010; Jennings and Iglesias 2002).

Cassava is considered a photosynthetically 'C_3–C_4

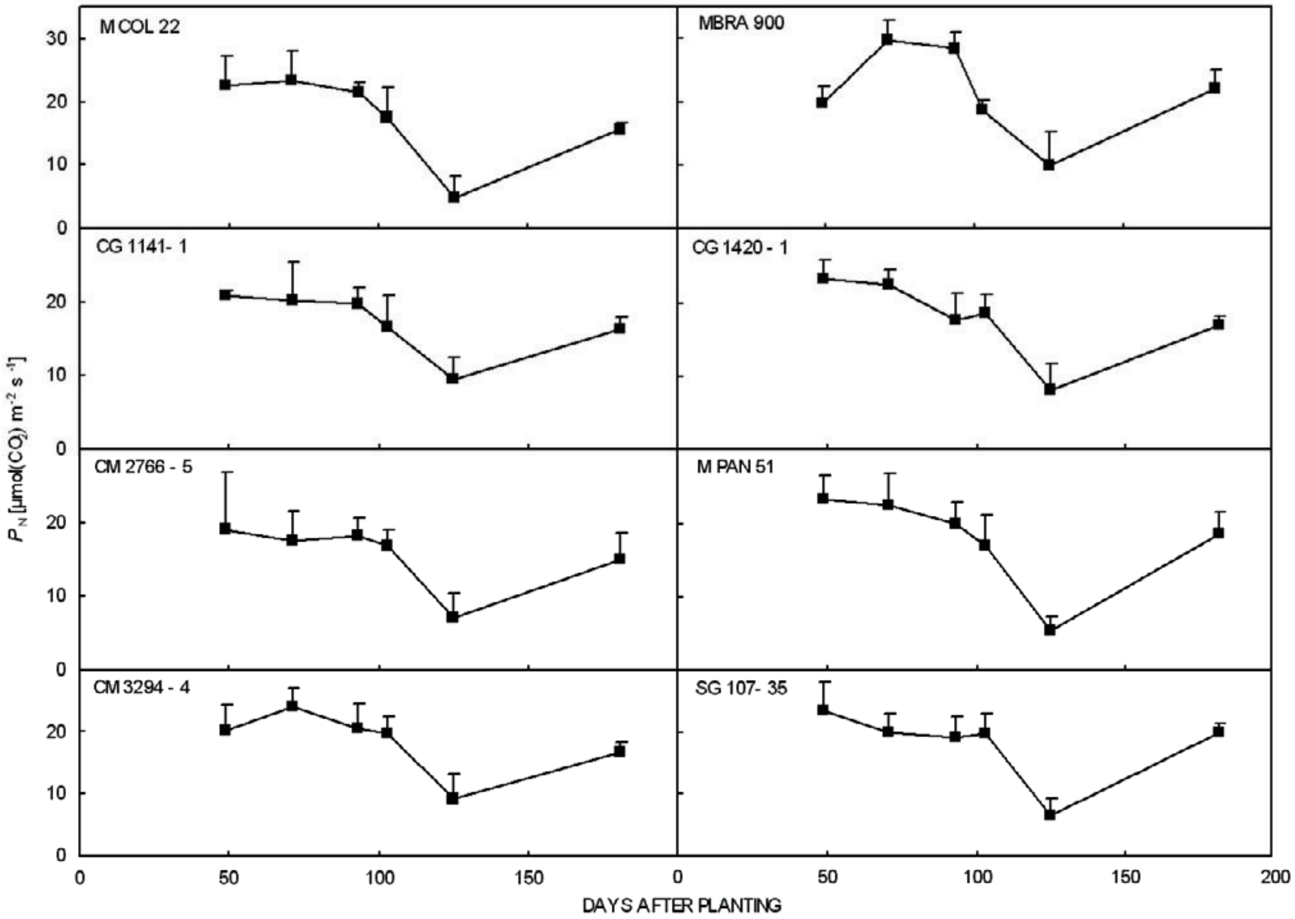

Fig. 8. Upper canopy leaf photosynthetic rate (P_N) of individual short cultivars. Data points are means ± SD ($n = 4$). Note the high maximum P_N in M Bra 900 (> 30 µmol(CO$_2$) m^{-2} s^{-1}), as compared to other cultivars.

intermediate' species (El-Sharkawy and Cock 1987a, El-Sharkawy 2006a). It has a high photosynthetic potential with maximum leaf photosynthetic rates that reach up to 42–50 µmol(CO$_2$) m^{-2} s^{-1}, as measured in normal air in several field-grown cultivars in favourable environments (wet soil, humid air, high irradiance and optimum temperature of 35°C) (El-Sharkawy *et al.* 1992a). Furthermore, cultivated cassava and wild relatives (*e.g.*, *M. rubricaulis* and *M. grahami*) have elevated activities of the C$_4$ PEPC (15–30% of activities in the C$_4$ maize and sorghum) (El-Sharkawy and Cock 1990, El-Sharkawy 2004, 2006a), which correlates with P_N and yield (El-Sharkawy *et al.* 2008). Moreover, *M. rubricaulis* and *M. grahami* have a unique leaf anatomy with a second palisade layer, albeit shorter than the upper long palisade layer, at the lower leaf side and possess numerous stomata on the upper surface (El-Sharkawy 2004), a rare characteristic in the mostly hypostomatous leaves of cultivated cassava (El-Sharkawy *et al.* 1984, 1985).These leaf characteristics (*i.e.* elevated activities of the C$_4$ PEPC and the double palisades coupled with the amphi-stomatous trait), could be used to further genetically improve P_N of short-stemmed cultivars. In absence of limiting irradiance interception (*i.e.*, near optimum LAI), upper canopy leaf P_N correlated with both total biomass and storage root yield over a wide range of cultivars and under different environments (El-Sharkawy and Cock 1990, El-Sharkawy *et al.* 1990, 2008, Pellet and El-Sharkawy 1993a, De Tafur *et al.* 1997a, El-Sharkawy 2007). Similar correlations were found across diploid, triploid, and tetraploid cassava cultivars grown in the Nigerian Savanna (Ekanayake *et al.* 2007).

Comparative crop nutrient uptake and NUE in tall and short cassava: Tables 2 and 3 summarize data on comparative nutrient uptake and NUE, in terms of storage root production, among short- and tall-stemmed cultivars. It is apparent that short-stemmed cultivars, as a group, have higher NUE for all major elements (14–24 % over values in tall cultivars, Table 2). This higher NUE is attributed, mainly, to smaller shoot biomass (Fig. 4, Table 1), and consequently, lesser total nutrient uptake (Table 3), as well as greater HI in short-stemmed cultivars (El-Sharkawy *et al.* 1998a). Also, it is possible that short-stemmed cultivars possess higher PNUE. These findings are of paramount importance for resource-limited cassava growers who rarely use fertilizers and mostly grow cassava on low-fertility soils without long period of fallow systems, thus, increasing pressures on dwindling natural resources (Fermont 2009, Fermont *et al.* 2008). Increasing yield per unit nutrient absorbed was a high-priority breeding objective that was addressed by both physiologists and breeders for decades at CIAT (Hershey and Jennings 1992, CIAT 1983-1998, Iglesias *et al.* 1995, El-Sharkawy 2004, 2006a). Hundreds of cassava accessions were screened over years for better adaptation to low-fertility soils, particularly in low-P acidic soils. Several cultivars, landraces and improved clones were identified with high tolerance levels to low-P and -K soils (CIAT 1983-1998, Hershey and Jennings 1992, Pellet and El-Sharkawy 1993a,b, 1997; Iglesias *et al.* 1995, El-Sharkawy and Cadavid 2000, El-Sharkawy 2004). Combining higher NUE, higher adaptation levels to low-fertility soils and high leaf photosynthesis (higher PNUE) in short-stemmed cassava cultivars should lead to both better productivity and conservation of soil fertility.

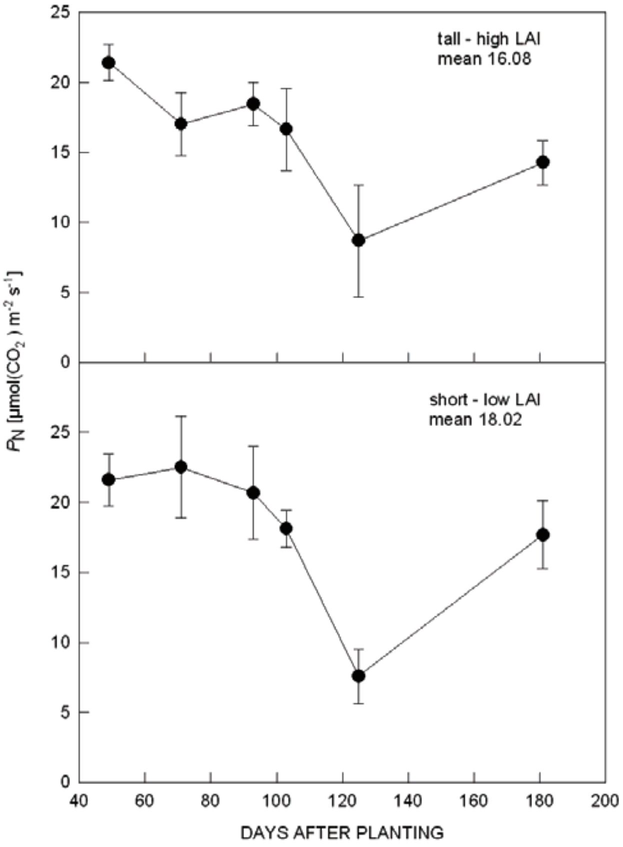

Fig. 9. Across cultivars average upper canopy leaf photosynthetic rate (P_N) for short and tall plant types. Data points are means ± SD (*n* = 28 for tall-stemmed cultivars, 32 for short-stemmed cultivars). Note the higher seasonal mean P_N in short cultivars. The large drop in P_N between 110–150 DAP was due to prolonged drought. After recovery from water stress (*i.e.*, 180 DAP), P_N remained higher in short types as compared to tall ones.

Conclusions: The research reported here was completed in 1996–1997, the short-stemmed variety, namely Portoviejo 650, was released in 1992, and the importance of the short stem phenomenon for drought tolerance, nutrient use efficiency, high photosynthetic capacity, and increased yields were quickly conveyed to cassava breeders. Subsequently, the breeders discussed all this in their scientific meetings (*e.g.*, Iglesias *et al.* 1995) and incorporated the short-stem gene(s) into their breeding programs. This achievement is of course similar to the semidwarfing genes used by N. Borlaug and H. Beachell in their International Programs of Wheat (at Mexico) and Rice (at Philippines), respectively. As such, dwarfism trait is as important a breakthrough for cassava as it was for wheat and rice.

Cassava is often perceived to be damaging to soils due its high productivity that leads to large exports of native nutrients, particularly from poor degraded soils (Howeler 1991, 2002; Ravi and Mohankumar 2004). Traditional cultivars are mostly tall, heavily branched with small HI (< 0.50) and large shoot biomass that accumulate substantial amounts of the nutrient absorbed from soils in their above-ground parts. From the present study and from previous published reports on cassava ecophysiology and agronomy, it may be concluded that plant structure, phenology, and morphology in cassava play an important role in crop physiology, breeding, and adaptability to stressful environments. Short-stemmed cultivars appear to have comparative advantages over tall ones in terms of yield per unit nutrient removed from soils [and perhaps a greater water use efficiency in terms of storage root production as shown by the observed trends in vegetative vigorous cultivars with much reduced shoot growth and greater storage root yields under extended water shortages (Connor *et al.* 1981, El-Sharkawy and Cock 1987b, El-Sharkawy *et al.* 1992b, El-Sharkawy and Cadavid 2002)], in leaf $P_{N,}$ in tolerance to low-fertility soils and in conserving native and/or applied nutrients. Because short-stemmed genotypes possess smaller leaf canopies (Table 1, Figs. 2,3), they should be planted at appropriate plant population densities (>10,000 plant ha^{-1}) that ensure seasonal near optimum LAI, and hence, maximize irradiance interception. This recommended cropping practice with improved short-stemmed cultivars might lead to greater yields than those obtained in tall ones due to the higher HI in the former plant types (Table 1). Additionally, high plant population densities in short-stemmed cassava cropping systems with rapid leaf canopy closure may reduce the frequency and the need for weeding as well as reducing soil erosion under intense tropical rainfalls often encountered at early crop growth stages, particularly in hillside cropping systems (Reining 1992, Ruppenthal *et al.* 1997, Lal 1997).

Since cassava resource-limited farmers rarely apply agrochemicals (Fermont 2009, Fermont *et al.* 2008, 2009, 2010) nor recycle plant residues to soils after harvest of storage roots and selection of planting materials, breeding programs should focus on selecting short- and medium-stemmed cultivars equipped with high leaf P_N, high NUE, longer leaf life [better leaf retention (El-Sharkawy *et al.* 1992b, Lenis *et al.* 2006)], high level of tolerance to diseases and pests, as well as earliness [early storage root formation and filling to ensure high dry matter contents in shorter growth cycle (Byju and Anand 2009)]. In seasonally dry and semi-arid ecozones, breeding and selection for extensive and deeper fine rooting systems should be combined with other desirable yield-related plant traits (El-Sharkawy 2007, 2010). These improved cultivars, when developed and adopted, are expected to further mitigate the predicted negative impact of the increasingly observed global climate changes upon agricultural productivity and food security in tropical regions (Rosenzweig and Parry 1994, Kamukondiwa 1996, IPCC 2006). In the tropics, global climate changes will probably intensify water deficits and prolong drought periods. In this case, enhancing 'water productivity' (defined as ratio of mass or value of product to volume or value of water depleted or diverted) (Kijne *et al.* 2004) by using water-use efficient cassava cultivars must be a top priority in tropical agricultural systems.

Table 2. Nutrient use efficiency (NUE) for root production at 10 months after planting for tall and short cassava cultivars. Values are means of each plant type group in two years. Note the greater NUE in short cultivars as compared to tall ones.

NUE [kg(dry root) kg^{-1}(total nutrient)]					
Group of cultivars	N	P	K	Ca	Mg
Tall	110	715	132	347	589
Short	131	885	161	430	669
Short/tall [%]	119	124	122	124	114

Table 3. Total plant nutrient uptake per land area and dry root production at 10 months after planting for tall and short cassava cultivars. Values are means of each plant type group in two years. Note the greater total nutrient uptake in tall cultivars as compared to short ones.

Total nutrient uptake (shoot and storage root)	[kg ha^{-1}]					[kg t^{-1}(dry root)]				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Tall	116	20	97	37	22	9.1	1.6	7.6	2.9	1.7
Short	76	11	61	23	15	7.1	1.1	6.2	2.3	1.5

Finally, an important concluding question arises for the attention of scientists/researchers, farmers and policy decision makers concerned with agriculture, food security and environmental issues: 'Would cassava be the promised crop in the nondistant future, not only as a poor man food crop in the tropics and subtropics, but also as a major source for renewable energy that will help in mitigating the negative effects of man-induced global climate changes *via* the overconsumption of atmosphere-polluting fossil fuels'? In comparative studies, Wang in China (2002) estimated that cassava has the highest biofuel potential among other possible major polysaccharides producing crops [*i.e.*, in bioethanol yield (l ha^{-1} year^{-1}): cassava 6,000; sugarcane 4,900; sweet sorghum 2,800; rice 2,250; maize 2,050; wheat 1,560; but see Johnston *et al.* (2009) for other estimates]. These estimates of bioethanol production, given near optimum growth conditions to maximize yields, might further substantiate the high 'photosynthetic capacity' of cassava usually expressed under favourable environments and its potential for sequestering atmospheric carbon dioxide, thus, contributing to mitigating global warming. Yet, under stressful environments (*i.e.*, poor soils and prolonged drought), none of the other crops mentioned will probably survive long enough and produce as much food and/or biofuel as cassava would produce. On behalf of humanity, our gratefulness is expressed for the 'Natives of the Americas' who since millennia had recognized the great potential of cassava as well as that of staples such as maize and potato.

References

Adeyemo, S.: Molecular Genetic Characterization of Photoperiodic Genes in Cassava (Manihot esculenta Crantz) and Attempts to Manipulate their Expression to Promote Floral Induction. – PhD Thesis. Univ. Köln, Köln 2009.

Allem, A.C.: The origin and taxonomy of cassava. – In: Hillocks, R. J., Thresh, J.M., Bellotti, A.C. (ed.): Cassava: Biology, Production and Utilization. Pp.1-16. CABI Publish., New York – Wallingford 2002.

Altieri, M. A., Liebman, M.: Insect, weed, and plant disease management in multiple cropping systems. – In: Francis, C. A.(ed.): Multiple Cropping Systems. Pp.183-218. Macmillan Publish. Co., New York – London 1986.

Alves, A. A. C.: Cassava botany and physiology. – In: Hillocks, R. J., Thresh, J. M., Bellotti, A.C. (ed.): Cassava: Biology, Production and Utilization. Pp. 67-89. CABI Publish., New York – Wallingford 2002.

Ayoola,O. T., Makinde, E.A.: Fertilizer treatment effects on performance of cassava under two planting patterns in a cassava-based cropping system in South West Nigeria. – Res. J. Agr. Biol. Sci. **3**: 13-20, 2007.

Borlaug, N. E.: Contributions of conventional plant breeding to food production. – Science **219**: 689-693,1983.

Byju, G., Anand, M.H.: Differential response of short-and long-duration cassava cultivars to applied mineral nitrogen. – J. Plant Nutr. Soil Sci. **172**: 572-576, 2009. doi: 10.1002/jpln.200800044

Cadavid, L.F., El-Sharkawy, M.A., Acosta, A., Sánchez, T.: Long-term effects of mulch, fertilization and tillage on cassava grown in sandy soils in northern Colombia. – Field Crops Res. **57**: 45-56, 1998.

CIAT: Cassava Program Annual Reports for 1983-1998. – Centro Internacional de Agricultura Tropical, Cali 1983–1998.

CIAT: Cassava Program Annual Report for 1993. – Centro Internacional de Agricultura Tropical, Cali 1993.

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

Cock, J.H., El-Sharkawy, M.A.: Physiological characteristics for cassava selection. – Exp. Agr. **24**: 443-448, 1988.

Cock, J.H., Franklin, D., Sandoval, G., Juri, P.: The ideal cassava plant for maximum yield. - Crop Sci. **19**:271-279, 1979.

Cock, J.H., Porto, M.C.M., El-Sharkawy, M.A.: Water use efficiency of cassava. III. Influence of air humidity and water stress on gas exchange of field grown cassava. – Crop Sci. **25**: 265-272, 1985.

Connor, D.J., Palta, J.: Response of cassava to water shortage. III. Stomatal control of plant water status. – Field Crops Res. **4**: 297-311, 1981.

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

De Tafur, S.M.: [Fisiología de la Yuca (*Manihot esculenta* Crantz). – In: Ospina, B., Ceballos, H. (ed.): Cultivo de la Yuca en el Tercer Milenio: Sistemas Modernos de Producción, Procesamiento, Utilización y Comercialización.] Pp. 34-45. Centro Internacional de Agricultura Tropical (CIAT), CLAYUCA, Cali 2002. [In Spanish]

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

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

Ekanayake, I.J., Dixon, A.G.O., Kasele, I.N., Noah, A.N.D.: Plant water relations and photosynthetic properties of polyploidy cassava grown in the Nigerian Savvana. – In: Kapinga, R., Kingamkono, R., Msabaha, M., Ndunguru, J., Lemaga, B., Tusiime, G. (ed.) : Proceedings of the Thirteenth Triennial Symposium of the International Society for Tropical Root Crops (ISTRC). Pp. 210-217. ISTRC, Arusha 2007.

Eke-Okoro, O.N., Njoku, D.N, Madu, A., Ezulike, T.O: Impact of global warming and crop factors on the growth and productivity of four cassava (*Manihot esculenta* Crantz) cultivars in Nigeria. – Sci. Res. Essays **4**: 955-960, 2009. http://www.academicjournals.org/sre

El-Sharkawy, M.A.: Effect of humidity and wind on leaf conductance of field grown cassava. – Rev. Bras. Fisiol. Veget. **2**: 17-22, 1990.

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

El-Sharkawy, M.A.: Cassava biology and physiology. – Plant Mol. Biol. **56**: 481-501, 2004.

El-Sharkawy, M. A.: 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 experimentalist's perspective. – Photosynthetica **43**: 161-176, 2005.

El-Sharkawy, M. A.: International research on cassava photosynthesis, productivity, eco-physiology, and responses to environmental stresses in the tropics. – Photosynthetica **44**: 481-512, 2006a.

El-Sharkawy, M. A.: Utility of basic research in plant/crop physiology in relation to crop improvement: a review and a personal account. – Braz. J. Plant Physiol. **18**: 419-446,2006b.

El-Sharkawy, M. A.: Physiological characteristics of cassava tolerance to prolonged drought in the tropics: Implications for breeding cultivars adapted to seasonally dry and semiarid environments. – Braz. J. Plant Physiol. **19**: 257-286, 2007.

El-Sharkawy, M.A.: Cassava: Physiological mechanisms and plant traits underlying tolerance to prolonged drought and their application for breeding cultivars in the seasonally dry and semiarid tropics. – In: Da Matta, F.M. (ed.): Ecophysiology of Tropical Tree Crops. Nova Science Publishers. Pp. 71-110. Hauppauge – New York 2010.

El-Sharkawy, M.A., Cadavid, L.F.: Genetic variation within cassava germplasm in response to potassium. – Exp. Agr. **36**: 323-334, 2000.

El-Sharkawy, M.A., Cadavid, L.F.: Response of cassava to prolonged water stress imposed at different stages of growth. – Exp. Agr. **38**: 333-350, 2002.

El-Sharkawy, M.A., Cadavid, L.F., De Tafur, S.M.: Nutrient use efficiency of cassava differs with genotype architecture. – Acta Agron. Univ. Nacional-Palmira-Colombia **48**: 23-32, 1998a.

El-Sharkawy, M.A., Cadavid, L.F., De Tafur, S.M., Caicedo, J.A.: Genotypic differences in productivity and nutrient uptake and use efficiency of cassava as influenced by prolonged water stress. – Acta Agron. Univ. Nacional-Palmira-Colombia **48**: 9-22, 1998b.

El-Sharkawy, M.A., Cock, J.H.: Water use efficiency of cassava. I. Effects of air humidity and water stress on stomatal conductance and gas exchange. – Crop Sci. **24**: 497-502, 1984.

El-Sharkawy, M.A., Cock, J.H.: The humidity factor in stomatal control and its effect on crop productivity. – In: Marcelle, R., Clijsters, H., van Poucke, M. (ed.): Biological Control of Photosynthesis. Pp. 187-198. Martinus Nijhoff Publ., Dordrecht – Boston – Lancaster 1986.

El-Sharkawy, M.A., Cock, J.H.: C_3-C_4 intermediate photosynthetic characteristics of cassava (*Manihot esculenta* Crantz). I. Gas exchange. – Photosynth. Res. **12**: 219-235, 1987a.

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

El-Sharkawy, M.A., Cock, J.H .:Photosynthesis of cassava (*Manihot esculenta* Crantz). – Exp. Agri. **26**: 325-340, 1990.

El-Sharkawy, M.A., Cock, J.H., De Cadena, G.: Stomatal characteristics among cassava cultivars and their relation to gas exchange. – Exp. Agr. **20**: 67-76, 1984.

El-Sharkawy, M.A., Cock, J.H., del Pilar Hernandez, A.: Stomatal response to air humidity and its relation to stomatal density in a wide range of warm climate species. – Photosynth. Res. **7**: 137-149, 1985.

El-Sharkawy, M.A., Cock, J.H., Lynam, J.K., del Pilar Hernandez, A., Cadavid L., L.F.: Relationships between biomass, root-yield and single-leaf photosynthesis in field-grown cassava. – Field Crops Res. **25**: 183-201, 1990.

El-Sharkawy, M. A., De Tafur, M. S.: 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, 2007.

El-Sharkawy, M.A., De Tafur, S.M., Cadavid, L.F.: Potential photosynthesis of cassava as affected by growth conditions. – Crop Sci. **32**: 1336-1342, 1992a.

El-Sharkawy, M.A., De Tafur, S.M., Cadavid, L.F.: Photosynthesis of cassava and its relation to crop productivity. – Photosynthetica **28**: 431-438, 1993.

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

El-Sharkawy, M. A., Lopez, Y., Bernal, L. M.: Genotypic variations in activities of phospho*enol*pyruvate carboxylase (PEPC) and correlations with leaf photosynthetic characteristics and crop productivity of cassava grown in low-land seasonally-dry tropics. – Photosynthetica **46**: 238-247, 2008.

Ernst-Schaeben, R.: Potential of Alley Cropping Maize and Cassava in South Benin, West Africa-Evaluation of the Establishing-Phase. – Ph.D. Thesis. Verlag Ulrich E. Grauer, Wendlingen 1994.

Essers, A.J.A.: Removal of Cyanogens from Cassava Roots: Studies on Domestic Sun-drying and Solid-substrate Fermentation in Rural Africa. – Ph.D. Thesis. Wageningen Agricultural University, Wageningen 1995.

FAOSTAT.: http://www.faostat.fao.org. 2007. Checked 11 October 2009.

Fermont, A. M.: Cassava and Soil Fertility in Intensifying Small holder Farming Systems of East Africa. – Ph.D. Thesis. Wageningen Agricultural University, Wageningen 2009.

Fermont, A.M., Tittonell, P.A., Baguma, Y., Ntawuruhunga, P., Giller, K.E.: Towards understanding factors that govern fertilizer response in cassava: lessons from East Africa. – Nutr. Cycl. Agroecosyst.: **86**: 133-151, 2010.

Fermont, A.M., van Asten, P.J.A., Giller, K.E.: Increasing land pressure in East Africa: The changing role of cassava and consequences for sustainability of farming systems. – Agri. Ecosyst. Environ. **128**: 239–250, 2008.

Fermont, A.M., van Asten, P.J.A., Tittonell, P.A., van Wijk, M. T., Giller, K.E.: Closing the cassava yield gap: an analysis from small-holder farms in East Africa. – Field Crops Res. **112**: 24-36, 2009.

Francis, C.A. (ed.): Multiple Cropping Systems. – Macmillan Publishing Co., New York – London 1986.

Fukuda, W.M.G., Ender, M., Iglesias, C.: Development of cassava germplasm for drier tropics and sub-tropical agro-ecosystems. – In: Annual Report 1992-1993, Working Plan 1993-1994. CNPMF, EPAGRI, CIAT; Cruz das Almas 1992–1993.

Hershey, C.H., Jennings, D.L.: Progress in breeding cassava for adaptation to stress. – Plant Breed. Abstr. **62**: 823-831, 1992.

Hillocks, R.J., Thresh, J.M., Bellotti (ed.): Cassava: Biology, Production and Utilization. – CABI Publishing, New York – Wallingford, UK 2002.

Howeler, R.H.: Long-term effect of cassava cultivation on soil productibity. – Field Crops Res. **26**:1-18, 1991.

Howeler, R.H.: Cassava mineral nutrition and fertilization. – In: Hillocks, R.J., Thresh, J.M., Bellotti, A.C. (ed.): Cassava: Biology, Production and Utilization. Pp 115-147. CABI Publishing, New York – Wallingford 2002.

Howeler, R.H., Cadavid, L.F: Accumulation and distribution of dry matter and nutrients during a 12-months growth cycle of cassava. – Field Crops Res. **7**: 123-139, 1983.

Howeler, R.H., Cadavid, L.F.: Short- and long-term fertility trials in Colombia to determine the nutrient requirements of cassava. – Fertilizer Res. **26**: 61-80, 1990.

Iglesias, C., Hershey, C., Calle, F., Bolanos, A.: Propagating cassava (*Manihot esculenta*) by sexual seed. – Exp. Agr. **30**: 283-290, 1994.

Iglesias, C., Bonierbale, M., El-Sharkawy, M., Lozano,L., Bellotti, A., Wheatley,C.: Focusing basic research for cassava varietal improvement. – In: Howeler, R.H. (ed.): Cassava Breeding, Agronomy Research and Technology Transfer in Asia. Pp. 40-60. Centro Internacional de Agricultura Tropical, Cali 1995.

Iijima, M., Izumi, Y., Yuliadi, E., Sunyoto, Ardjasa, W.S.: Cassava-based intercropping systems on Sumatra Island in Indonesia: Productivity, soil erosion and rooting zone. – Plant Prod. Sci. **7**: 347-355, 2004.

IPCC: Intergovernmental panel on climate change: IPCC special report on the regional impact of climate change. An assessment of vulnerability. -UNEP, WMO, 2006. Online (http://www.grida.no/climate/ipcc/regional/502.htm).

Jansson, C., Westerbergh, A., Zhang, J.M., Hu, X.W., Sun, C.X.: Cassava, a potential biofuel crop in (the) People's Republic of China. – Appl. Energy **86**: S95-S99, 2009.

Jennings, D.L., Iglesias, C.: Breeding for crop improvement. – In: Hillocks ,R.J., Thresh, J.M., Bellotti, A.C.(ed.): Cassava: Biology, Production and Utilization. Pp.149-166. CABI Publishing, New York – Wallingford 2002.

Johnston, M., Foley, J.A., Holloway, T., Kucharik, C., Monfreda, C.: Resetting global expectations from agricultural biofuels. – Environ. Res. Lett. **4**: 1-9, 2009. doi:10.1088/1748-9326/4/1/014004

Kamukondiwa, W.: Alternative food crops to adapt to potential climate change in southern Africa. – Clim. Res. **6**: 153-155, 1996.

Kawano, K.: Thirty years of cassava breeding for productivity - Biological and social factors for success. – Crop Sci. **43**: 1325-1335, 2003.

Kijne, J.W., Barker, R., Molden , D. (ed.).: Water Productivity in Agriculture: Limits and Opportunities for Improvement. – CAB International, Wallingford – Cambridge – Sri Lanka 2004.

Lal, R.: Soil degradative effects of slope length and tillage method on alfisols in Western Nigeria. II. Soil chemical properties, plant nutrient loss and water quality. – Land Degrad. Develop. **8**: 221-244, 1997.

Lebot, V.: Tropical Root and Tuber Crops: Cassava, Sweet Potato, Yams and Arides. – CABI International, Wallingford – Cambridge 2009.

Leihner, D.: Management and Evaluation of Intercropping Systems with Cassava. – Centro Internacional de Agricultura Tropical, Cali 1983.

Leihner, D.: Agronomy and cropping systems. – In: Hillocks, R.J., Thresh, J.M., Bellotti, A.C. (ed.): Cassava: Biology, Production and Utilization. Pp 91-113. CABI Publishing, New York – Wallingford 2002.

Lenis, J.I., Calle, F., Jaramillo, G., Perez, J.C., Ceballos, H., Cock, J.H.: Leaf retention and cassava productivity. – Field Crops Res. **95**: 126-134, 2006.

Madeley, J.: Breeding for the tough spots: CGIAR researchers are developing crops that thrive in the harshest habitats. – CERES-FAO Review: **26**: 22-26, 1994.

Oguntunde P.G.: Whole-plant water use and canopy conductance of cassava under limited available soil water and varying evaporative demand. – Plant Soil **278**: 371-83, 2005.

Oguntunde P.G., Alatise M.O.: Environmental regulation and modelling of cassava canopy conductance under drying root-zone soil water. – Meteorol. Appl. **14**: 245-252, 2007.

Orek, C., Zhang, P., Gruissem,W., Ferguson, M., Vanderschuren, H.: Gene expression associated with 'staygreen' trait for drought tolerance in cassava (*Manihot esculenta* Crantz). – Online 2008. http://www.northsouth.ethz.ch/news/past_events/ann_conf_08/WFC4_Orek.pdf

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

Pellet, D., El-Sharkawy, M.A.: Cassava varietal response to phosphorus fertilization. 2. Phosphorus uptake and use efficiency. – Field Crops Res. **35**: 13-20, 1993b.

Pellet, D., El-Sharkawy, M.A.: Cassava varietal response to fertilization: growth dynamics and implications for cropping sustainability. – Exp. Agr. **33**: 353-365, 1997.

Porto, M.C.M.: Physiological Mechanisms of Drought Tolerance in Cassava (*Manihot esculenta* Crantz). – Ph.D. Thesis. University of Arizona, Tucson 1983.

Pujol, B., Salager, J-L., Beltran, M., Bousquet, S., McKey, D.: Photosynthesis and leaf structure in domesticated cassava (Euphorbiaceae) and a close wild relative: have leaf photosynthetic parameters evolved under domestication? – Biotropica **40**: 305-312, 2008.

Ramanujam, T.: Effect of moisture stress on photosynthesis and productivity of cassava. – Photosynthetica **24**: 217-224, 1990.

Ravi, V., Mohankumar, C. R.: Cassava-based multiple cropping systems. – Hort. Rev. **30**: 355-500, 2004.

Reining, L.: Erosion in Andean Hillside Farming. – Verlag Josef Margraf, Weikersheim 1992.

Romanoff, S., Lynam, J.: Cassava and African food security: Some ethnographic examples. – Ecol. Food Nutr. **27**: 29-41, 1992.

Rosenzweig, C., Parry, M.L.: Potential impact of climate change on world food supply. – Nature **367**: 133-138, 1994.

Ruppenthal, M., Leihner, D.E., Steinmüller, N., El-Sharkawy, M.A.: Losses of organic matter and nutrients by water erosion in cassava-based cropping systems. – Exp. Agr. **33**: 487-498, 1997.

Salekdeh, G.H., Reynolds, M., Bennett, J., Boyer, J.: Conceptual framework for drought phenotyping during molecular breeding. – Trends Plant Sci. **14**: 488-496, 2009.

Sangakkara, U.R., Attanayake, K.B., Gajanayake, J.N. and Bandaranayake ,P.S.D.R.: Impact of mulches on growth and yields of cassava and sweet potato in tropical Asia. –In: New directions for a diverse planet: Proceedings of the 4th International Crop Science Congress Brisbane, Australia, Brisbane 2004. www.cropscience.org.au/icsc2004/.../380_sangakkarar.htm

Sarma, F. W., Kunchai, D.: Trends and Prospects for Cassava in the Developing World. – International Food Policy Research Institute, Washington 1991.

Setter, T.L. , Fregene, M.A. : Recent advances in molecular breeding of cassava for improved drought stress tolerance. – In: Jenks, M.A., Hasegawa, P.M., Jain, S.M. (ed.): Advances in Molecular Breeding Toward Drought and Salt Tolerant Crops. Pp. 701-711. Springer, New York 2007.

Sinkevičienė, A., Jodaugienė, D., Pupalienė, R., Urbonienė, M.: The influence of organic mulches on soil properties and crop yield. – Agron. Res. **7**: 485–491, 2009. www.eau.ee/~agronomy/vol07Spec1/p7sI53.pdf

Splittstoesser, W.E., Tunya, G.O.: Crop physiology of cassava. – Hort Rev. **13**: 105-129, 1992.

Tscherning, K., Leihner, D.E., Hilger, T.H., Müller-Sämann, K.M., El-Sharkawy, M.A.: Grass barriers in cassava hillside cultivation: Rooting patterns and root growth dynamics. – Field Crops Res. **43**: 131-140, 1995.

Veltkamp, H.J: Physiological Causes of Yield Variation in Cassava (*Manihot esculenta* Crantz). – PhD.Thesis. Agricultural University, Wageningen 1985.

Visarada, K.B.R.S., Meena, K., Aruna, C. Srujana, S., Saikishore, N., Seetharama, N.: Transgenic breeding: perspectives and prospects. – Crop Sci. **49**: 1555-1563, 2009.

Wang, W.: Cassava production for industrial utilization in China - present and future perspective. – In: Cassava Research and Development in Asia: Exploring new Opportunities for an Ancient Crop. Pp. 33-38. Seventh regional cassava workshop, Bangkok, Thailand. Bangkok 2002.

Zhang, P., Wang, W.-Q., Zhang, G-L., Kaminek, M., Dobrev, P., Xu, J., Gruissem, W.: Senescence-inducible expression of isopentenyl transferase extends leaf life, increases drought stress resistance and alters cytokinin metabolism in cassava. – J. Integ. Plant Biol. (JIPB), China. (in press), 2010. http://www.jipb.net/1291369783750000.pdf

Zöbisch, M.A., Richer, C., Heiligtag, B., Schlott, R.: Nutrient losses from cropland in the central highlands of Kenya due to surface runoff and soil erosion. – Soil Tillage Res. **33**: 109-116, 1995.