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Photosynthesis in drought-adapted cassava

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Abstract

After 45 d of limited water supply, cassava (*Manihot esculenta* Crantz) exhibited pronounced reduction in shoot growth, high leaf fall, and decreased stomatal conductance. However, the water status of the remaining leaves was unaffected. This was combined with an amplified heliotropic response and drooping which minimises radiant energy interception at mid-day, suggesting that leaves are sensitive to high irradiance (I). In well-irrigated plants, CO_2-saturated oxygen evolution and net photosynthetic rate (P_N) in air were markedly higher (5-fold) in young (expanding) leaves than in mature leaves. Water limitation did not strongly modify CO_2-saturated oxygen evolution but it altered P_N in air for both types of leaves, although differently. The mature leaves of drought-adapted plants displayed residual rate of P_N and deteriorated photosystem 2 (PS2) photochemistry estimated from chlorophyll (Chl) *a* fluorescence measurements. In young leaves at moderate I, P_N was depressed by only 66 % in stressed plants. Moreover, the photochemical quenching of Chl *a* fluorescence and the quantum efficiency of PS2 photochemistry in young leaves were comparable in both control and stressed plants. In contrast at high I, P_N was almost null and marked decreases in the two fluorescence parameters were apparent. Hence the strong heliotropic response and drooping displayed by young leaves under water limitation is an important strategy for avoiding inactivation of P_N by high I and therefore for cassava tolerance to drought.

Additional key words: chlorophyll fluorescence; light stress; *Manihot esculenta*; young and mature leaves.

Introduction

A low rate of P_N in plants suffering from water stress has been often reported (Kaiser 1987). Both stomatal and non-stomatal factors contribute to the effects of drought on P_N. Stomatal closure is the main factor since the photosynthetic apparatus is largely unaffected by water limitation in whole plants or by direct desiccation in excised leaves (Cornic *et al.* 1992, Tourneux and Peltier 1995). Changes in stomatal aperture affect water loss proportionally more than P_N, hence improving water use efficiency (WUE) (Gimenez *et al.* 1992, Martin and Ruiz-Torres 1992).

Cassava, which must endure several months of natural drought during its seasonal cycle, is tolerant to long periods of water shortage. The plant resists drought by reducing its leaf canopy and closing its stomata. This is combined with a strong heliotropic response whereby the plant leaves orient in such a way that they seek maximum I interception when the vapour pressure deficit (VPD) is small and solar radiation is low. However, they intercept less photons at midday when the VPD and I are high. This behaviour is observed in mature leaves of well-watered plants but is much more pronounced in plants suffering from shortage of water (Cock *et al.* 1985, Yao *et al.* 1988, El-Sharkawy *et al.* 1992a, El-Sharkawy 1993).

Chl *a* fluorescence analysis can be used to monitor changes in the functioning and the regulation of the photosynthetic apparatus. The yield of Chl *a* fluorescence is determined by two distinct quenching processes, the photochemical quenching (q_P) and the nonphotochemical quenching (q_{NP}). The q_P is due to the operation of the photosynthetic electron transport. The q_{NP} arises from nonradiative dissipative processes that function in the regulation of PS2 photochemistry. These processes compete effectively with the excitation energy transfer processes in PS2, which leads to reduced

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quantum yield but allows PS2 to remain relatively oxidized when the transport of electrons is low (Bradbury and Baker 1981, Schreiber *et al.* 1986, Horton and Hague 1988, Foyer *et al.* 1990, Genty *et al.* 1990). Effectively, q_{NP} dissipates the excess of energy in leaves that experience various stresses, but the mechanism is not general. It differs among species and according to the type of stress and adaptation of the plant (Genty *et al.* 1987, Khamis *et al.* 1990, Ögren 1990, Baker 1991, Scheuermann *et al.* 1991, Jefferies 1994).

In the present paper, the effect of water stress on P_N and PS2 photochemistry in leaves of drought-adapted cassava plants was examined. Since the heliotropic response and drooping prevents the leaves of water-deficient cassava from being exposed to high I, another objective of the study was to examine the susceptibility of PS2 to I through its activity estimated *in vivo* from Chl *a* fluorescence measurements.

Materials and methods

Plants: Cassava (*Manihot esculenta* Crantz cv. CM 1585-13) plants were derived from a clone provided by CIAT (Cali, Colombia), cross parents (M Col 22×M Ven 270) × (M Col 22×M Col 647), and propagated by *in vitro* culture. The plants were grown in individual (15 000 cm^3) plastic pots, containing mixed peat and sand, in a glasshouse in Montpellier (South of France, 43° latitude). The environmental conditions were approximately 30/25 °C (day/night) with natural photoperiod (between 13 to 16 h), solar I (inferior to 1000 µmol m^{-2} s^{-1}), and 70-80 % relative humidity. The plants were watered three times a week with 1200 cm^3 of distilled water and with a complete nutrient solution each month. Three-month-old plants (10 replicates per treatment) were used for measurements in both young, expanding leaves, and mature leaves (Fig. 1). The experiment was duplicated.

Treatments, sampling and assay: Water stress was imposed in the glasshouse by decreasing the irrigation volume from 1 200 (control) to 80 (stress) cm^3. After a 45-48-d treatment, the morphological characteristics of the plants and the water status of leaves sampled before dawn and at midday were determined. The leaf water potential (Ψ) was obtained on a leaf portion using a hydraulic press according to Hunt *et al.* (1984). The relative water content (RWC) and the water content (WC) were measured according to Tyree (1976) and defined as follows: RWC = (fresh mass at Ψ - dry mass)/(fresh mass at Ψ = 0 - dry mass), and WC = (fresh mass at Ψ)/(dry mass).

The P_N was measured in the glasshouse between 3 and 5 h after dawn under I of *ca.* 300 or 1000 µmol m^{-2} s^{-1} using a portable gas analyser (*LI-6200, LI-COR*, Lincoln, USA) on attached leaves. The low I was simply achieved by respecting the natural orientation of leaves at the beginning of measurement period. By contrast, high I was acquired by forcing the leaves to orient in such a way that they seek maximum photon interception later in the morning. P_N was determined after maintaining the leaf for 3 to 4 min until the assimilation was constant. The stomatal conductance (g_s) of the lower leaf surface was measured using an automatic porometer (*Mk3, Delta-T Devices*, Cambridge, England). CO_2-saturated oxygen evolution was estimated with a leaf disc electrode (*LD2, Hansatech*, Norfolk, England) by measuring oxygen change as a function of I as reported by Walker (1987) before Chl determination (Khamis *et al.* 1990).

Leaf tissues were sampled in the morning, immediately frozen in liquid nitrogen, and stored at –80 °C. Phosphoglycolate phosphatase activities were assayed colorimetrically by determining the ortho-phosphate released using a modified Fiske-Subbarow procedure as described by Baldy *et al.* (1989).

After rapid transfer of the plants from the glasshouse to an adjacent laboratory, fluorescence yield was measured after 30 min dark acclimation at temperature similar to that of the glasshouse, in air, on the attached leaves and using a pulse amplitude modulation fluorometer (*Hansatech, MFMS*, Norfolk, England). The analyses of fluorescence were performed using the light-doubling technique (Bradbury and Baker 1981, Genty *et al.* 1989). The quantum efficiency of PS2 photochemistry was estimated as follows: $\Phi_{PS2} = (F_m' - F_s')/F_m'$ where F_m' is the pulse-saturated fluorescence yield in the light (when all the PS2 trap are closed), and F_s' is the steady-state fluorescence yield in the light. Photochemical quenching (q_P) and non-photochemical quenching (q_{NP}) of Chl *a* fluorescence were estimated as follows: $q_P = (F_m' - F_s')/(F_m' - F_0')$, and $q_{NP} = (F_m - F_m')/F_m$ where F_0' is the lowest fluorescence yield with open PS2 centres (after dark imposition), and F_m the highest pulse-saturated fluorescence yield in the dark-adapted state.

Results

Shoot development was markedly affected by 45 d of water deficiency (Fig. 1, Table 1). The stems stopped growing from the onset of the period of water limitation. The number of leaves per plant decreased because of a dramatic acceleration of leaf senescence and fall, and a substantial decrease in leaf emergence. In addition, the area of leaves that emerged and expanded during the drought period was about half that of the control. These results obtained in a glasshouse are in agreement with previous findings in field experiments (Cock *et al.* 1985, Yao *et al.* 1988, El-Sharkawy *et al.* 1992b, El-Sharkawy 1993, and our observations in the Congo, ORSTOM Centre Brazzaville, during the dry season). This demonstrates that our experimental conditions mimic field conditions well.

Fig. 1. Four-month-old cassava plant grown on a mixture of standard peat and sand in a glasshouse (*A*) in optimal water availability (control) or (*B*) after 45-48 d of water limitation (stressed). Water stress was imposed by lowering the irrigation volume delivered 3 times a week from 1200 to 80 cm^3. Typical "young" (expanding, 2 weeks old) and "mature" (fully expanded, 8-10 weeks old) leaves are indicated by *arrows*.

Table 1. Shoot characteristics of 4-month-old cassava plants grown with high or low water availability for 45 d. The total number of fallen and emerged leaves per plant, the area of mature leaves expanded during the treatment, and the height of plant stems were determined. At the beginning of the experiment, plant height was *ca.* 95 cm with 19 leaves. Means ± SE. Treatments and experimental conditions are given in the legend of Fig. 1.

Treatment	Leaves Fallen	emerged	Area of mature leaves [cm^2]	Height of stem [cm]
Control	6±0.9	12 ± 0.9	129 ± 7.6	141 ± 2.2
Stress	13±0.9	5 ± 0.4	66 ± 8.0	97 ± 2.2

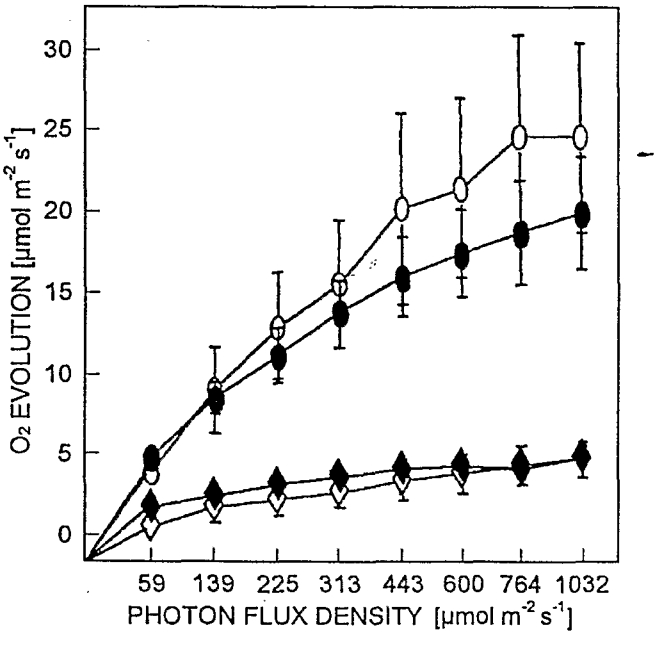

Fig. 2. Effect of water limitation on light saturation curves of O_2 evolution in young and mature leaves of cassava plants. O_2 evolution was estimated at saturating CO_2 on leaf-discs. Means ± SE. Treatment and experimental conditions are given in the legend of Fig. 1. *Open symbols*: control; *closed symbols*: stressed plants; *circles*: young leaves, *squares*: mature leaves.

The exposure of plants to water stress did not result in a significant decrease in water potential in either young or mature leaves measured before dawn and at midday. This was observed using a hydraulic press (Table 2) or by the pressure bomb technique (Scholander *et al.* 1965, values not shown). Water limitation slightly decreased WC and RWC in young leaves whereas no difference in these parameters was observed in mature leaves (Table 2). This probably was because the stomata of young leaves of water deficient plants were partially open, thus allowing CO_2 assimilation but also water loss (see below).

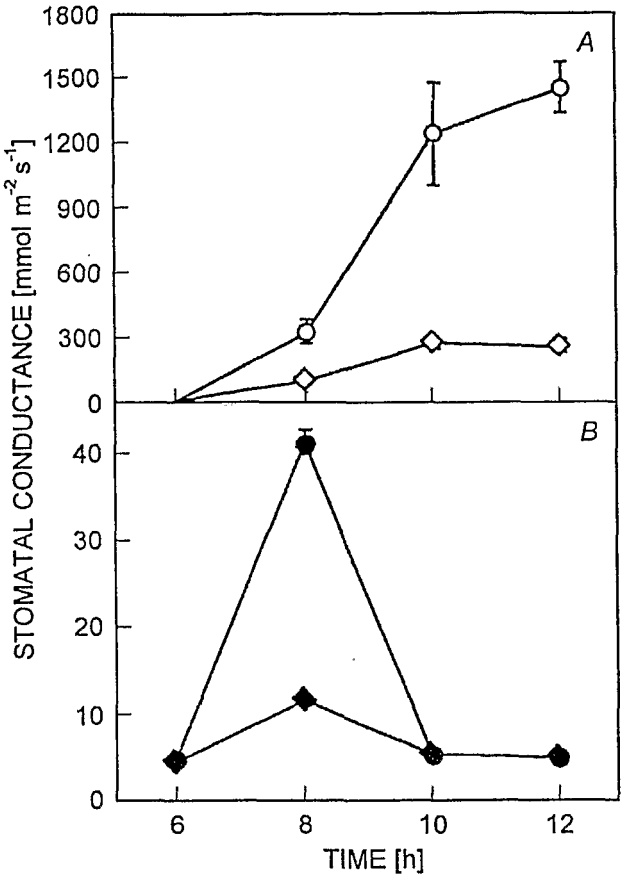

Fig. 3. Changes in stomatal conductance of lower leaf surface of young and mature leaves of control (*A*) and water stressed (*B*) cassava plants from pre-dawn until mid-day. Means ± SE. Treatments and experimental conditions are given in the legend of Fig. 1. *Open symbols*: control; *closed symbols*: stressed plants; *circles*: young leaves, *squares*: mature leaves.

Fig. 2 illustrates the response of oxygen evolution for leaf discs with a saturating CO_2 concentration. In control and water-stressed plants, the young leaves exhibited a higher maximum rate of oxygen evolution than mature leaves. Water stress reduced oxygen evolution in young leaves at high *I*, the rate at 1000 μmol m^{-2} s^{-1} being only 75 % of that of the control, however, there were large variations within leaves of the same water treatment. The rate of oxygen evolution in mature leaves was very low and similar in control or stressed plants.

g_s increased until midday in young leaves of control plants (Fig. 3). It was always significantly higher than in mature leaves, whose conductance reached a relatively constant value after 3 h during the light period. g_s was very low under water limitation, irrespective of leaf age. A small, transitory increase was nevertheless detectable in young leaves at the beginning of morning.

In leaves of control plants under low *I* (intercepted respecting the natural orientation of the leaves), P_N was almost five times higher in young than mature leaves (Table 3). At high *I* (1000 μmol m^{-2} s^{-1}, achieved by forcing the leaves to orient to seek maximum photon interception), P_N was increased (about two-fold) in both types of leaves. Under water deficit and low *I*, P_N decreased by 66 % in young leaves and by more than 90 % in mature leaves as compared to the controls. At high *I*, P_N was hardly detectable in stressed plants irrespective of leaf age. Shortage of water had only a weak depressive effect—if any—on leaf chlorophyll content but it markedly increased *in vitro* phosphoglycolate phosphatase activity in young leaves (Table 3).

Table 2. Leaf water status measured before dawn and at midday in young and mature leaves of control or water-stressed cassava plants. Means ± SE. WC: water content [kg kg^{-1}(d.m.)]; RWC: relative water content; Ψ: leaf water potential [MPa]. Treatments and experimental conditions are given in the legend of Fig. 1.

Plants	Leaves	WC		RWC		Ψ	
		pre-dawn	mid-day	pre-dawn	mid-day	pre-dawn	mid-day
control	young	5.3 ± 0.3	4.2 ± 0.1	0.91 ± 0.02	0.91 ± 0.03	-0.06 ± 0.01	-0.09 ± 0.01
	mature	3.6 ± 0.1	3.5 ± 0.2	0.94 ± 0.01	0.88 ± 0.04	-0.32 ± 0.01	-0.33 ± 0.03
stressed	young	3.9 ± 0.2	3.7 ± 0.1	0.87 ± 0.01	0.86 ± 0.01	-0.09 ± 0.02	-0.07 ± 0.01
	mature	3.8 ± 0.4	3.5 ± 0.3	0.95 ± 0.00	0.90 ± 0.01	-0.31 ± 0.02	-0.23 ± 0.02

The relative contributions of photochemical (q_P) and non-photochemical (q_{NP}) quenching in determining Φ_{PS2} during the induction of photosynthesis in attached leaves are shown in Fig. 4. In young leaves at low *I*, the steady-state values of q_P and q_{NP} at the end of induction period were fairly similar in stressed and control plants and hence the Φ_{PS2} values were comparable. Upon transition from low to high *I*, q_{NP} was higher in steady state in both

types of plants. The increase in q_{NP} was not modified by drought. Values of q_P decreased with increase in I. This is the normal response of q_P. However, in control plants, increasing I caused a substantial and rapid, but transient fall in q_P. The decrease was greater in stressed plants and q_P did not recover. Accordingly, at high I in young leaves, Φ_{PS2} was severely affected as a result of water stress.

Chl *a* fluorescence analysis revealed substantial differences between mature and young leaves. The steady state values reached by q_P and Φ_{PS2} in the control plants at low I were lower in mature leaves than in young leaves. Water deficiency depressed these parameters further in mature leaves. At high I in mature leaves, q_P and Φ_{PS2} were very low in both control and stressed plants.

Table 3. Net photosynthetic rate (P_N) in normal air, chlorophyll contents, and *in vitro* phosphoglycolate phosphatase activities of leaves of cassava plants grown under sufficient or limited water availability. P_N was determined 4-5 h after dawn at low and high irradiances (PFD of *ca.* 300 and 1000 μmol m^{-2} s^{-1}, respectively). Measurements were made in young and mature leaves. Means ± SE. Treatments and experimental conditions are given in the legend of Fig. 1. nd: non-detectable, tr: traces of activity.

Leaves	P_N [μmol(CO_2) m^{-2} s^{-1}]				Chlorophyll [mg m^{-2}]		Phosphoglycolate phosphatase [mmol kg^{-1}(Chl) s^{-1}]	
	300 μmol m^{-2} s^{-1}		1000 μmol m^{-2} s^{-1}					
	control	stress	control	stress	control	stress	control	stress
young	12.2 ± 0.5	4.0 ± 0.9	23.9 ± 0.5	0.1 ± 0.1	676 ± 123	617 ± 44	tr	5.6 ± 2.4
old	2.6 ± 0.6	0.2 ± 0.1	4.0 ± 0.1	nd	467 ± 82	454 ± 114		

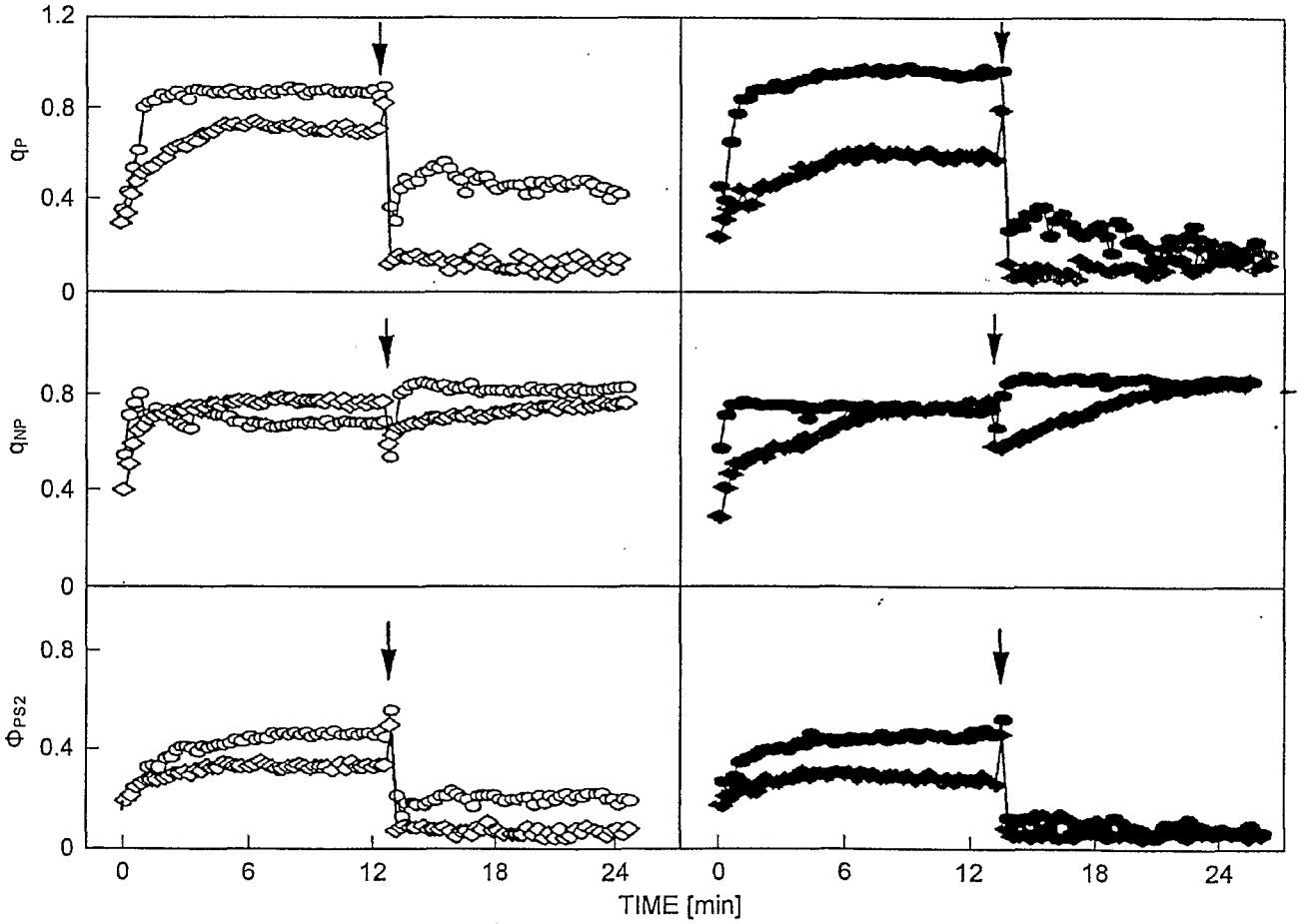

Fig. 4. Effect of water deficiency on chlorophyll (Chl) *a* fluorescence at room temperature. The chemical quenching coefficient (q_P), the non-chemical quenching coefficient (q_{NP}), and the quantum efficiency of PS2 photochemistry (Φ_{PS2}) were observed during the induction phase of photosynthesis at low irradiance (220 μmol m^{-2} s^{-1}) with a subsequent transition to high (1000 μmol m^{-2} s^{-1}) irradiance. The experiments were carried out with attached young (*circles*) or mature (*squares*) leaves of stressed (*dark symbols*) or control (*open symbols*) cassava plants. *Arrows* indicate the point of transition in irradiance. Means ± SE. Treatment and experimental conditions are given in the legend of Fig. 1.

Discussion

In mature leaves of plants grown with sufficient water supply, both the oxygen evolution at saturated CO_2 and P_N in normal air (Fig. 2, Table 3) were unusually low as compared to other studies on cassava grown out-door in pots or in the field (El-Sharkawy, unpublished). These low P_N values could be due to shade effects combined with the relatively low I (maximum of 1000 μmol m^{-2} s^{-1}) used for growth in our glasshouse compared to the experimental conditions used by El-Sharkawy *et al.* (1992b) with I of 1 200 to 2 000 μmol m^{-2} s^{-1}. However, mature leaves of cassava displayed lower P_N than young leaves (De Tafur *et al.* 1997). Furthermore in mature leaves, fluorescence analysis showed altered PS2 photochemistry, with low q_P and Φ_{PS2} values. Thus the primary electron acceptor of PS2, Q_A, was strongly reduced in mature leaves (especially under high I).

In contrast with mature leaves, young leaves of control plants exhibited high P_N. These leaves also showed fluorescence parameters typical for healthy leaves both under low (300 μmol m^{-2} s^{-1}) and high (1000 μmol m^{-2} s^{-1}) I. Indeed, following a transition from low to high I, they behaved normally, with enhanced P_N and q_{NP} values, allowing q_P to remain relatively high, and preventing excessive accumulation of light-generated reductant. Nevertheless, P_N in combination with the leaf area determined carbon uptake. Owing to the respective proportions of the two types of leaves (mature and young), overall CO_2 assimilation in well-watered plants was mainly accounted for by mature leaves.

Cassava plants adapt to water shortage by a rapid, large decrease in their evaporative surface. They also react by partially closing their stomata, and hence increasing WUE (Cock *et al.* 1985, Chaves and Pereira 1992, El-Sharkawy *et al.* 1992a, El-Sharkawy 1993). These stress avoidance mechanisms are not special in themselves but they are marked and extremely effective in this species. Indeed, the water status of the remaining leaves (young and mature) was little affected after 45-d water deficit. Such remarkable stable leaf water potential in cassava undergoing changes in water environment has already been described (Cock *et al.* 1985, El-Sharkawy 1993, De Tafur *et al.* 1997).

In water-stressed plants under low I, P_N was maintained only in the young leaves whereas it was almost nil in mature leaves. This probably resulted from stomatal factors (see Fig. 3) since CO_2-saturated oxygen evolution in mature leaves was not greatly affected by water shortage. Thus, in water-deprived plants, both the acceleration of the shedding of mature leaves and the pronounced decrease in P_N in these leaves mean that most of the carbon nutrition of the plant had to be provided by the young leaves. The latter clearly play a central role in the adaptation of cassava to the stressful environment.

CO_2-saturated oxygen evolution is usually affected only in leaves suffering from severe water stress with a RWC value of less than 70 % (Kaiser 1987, Cornic *et al.* 1989, Havaux 1992). CO_2-saturated oxygen evolution of young leaves of water-deficient cassava plants was decreased by 25 % despite their relatively high RWC. Photoinhibition can affect the maximal rate of oxygen evolution (Long *et al.* 1994). A decrease in the ratio $(F_m - F_0)/F_m$ shows that the leaf has been photoinhibited (Björkman and Powles 1984, Long *et al.* 1994). Our measurements of this ratio showed that photoinhibition could not mainly account for the decreased capacity of these leaves as compared to the control ($F_m - F_0/F_m$ was about 0.5 for both types of plants). The decreased maximal oxygen evolution in young leaves may have resulted from a reduction in the Calvin cycle capacity as found in some species under water stress (Ögren 1988, Gimenez *et al.* 1992, Martin and Ruiz-Torres 1992). However, in spite of this decrease, the capability of the photosynthetic machinery remained largely in excess of that required to support the observed P_N (Fig. 2, Table 3), and the decrease in P_N observed in young leaves following water shortage resulted mainly from their very low g_s (Fig. 3).

Young leaves displayed consistent but reduced P_N under water stress and low I. No significant difference between stress and non-stress conditions was detected in the Chl *a* fluorescence parameters (Fig. 4). This may result from an increase in the rate of reactions (other than those of the Calvin cycle) which consume photosynthetically generated electrons such as photorespiration, although it is not always the main process for avoiding over-reduction of the electron transport chain (Genty *et al.* 1987, Havaux 1992, Biehler and Fock 1996). In young leaves of cassava, indirect evidence of a possible increase in rate of photorespiration during drought stress was derived from *in vitro* measurements of the activity of phosphoglycolate phosphatase (Table 3). This enzyme is involved in hydrolysis of the phosphoglycolate formed by ribulose-1,5-bisphosphate (RuBP) oxygenation which initiates the photorespiratory pathway. The phosphoglycolate phosphatase activity in control leaves was extremely low. However, cassava leaves have reduced photorespiration under well watering (El-Sharkawy and Cock 1990, El-Sharkawy *et al.* 1992a).

We can compare the electron transport rates estimated from fluorescence measurement (J_f) with the theoretical minimum rates for CO_2 assimilation (J_c) calculated from gas-exchange measurement (cf. Table 3 and Fig. 4). J_f was estimated by multiplying the quantum yield of PS2 electron transport by I. The result was multiplied by 0.4 because leaves typically have an absorptance of 0.8 and because it was assumed that

incident radiation is equally distributed to the photosystems. J_c is based on P_N (neglecting dark respiration) multiplied by 4 since there is a minimum requirement of 4 electrons per CO_2 fixed in photosynthesis. In young leaves of control plants, under high or low I, J_f was 55 and 80 μmol m^{-2} s^{-1}, and J_c was 49 and 96 μmol m^{-2} s^{-1}, respectively. Thus the rates of electron flow for carbon assimilation are very similar to those calculated from PS2 activity. This is consistent with a low activity of reactions other than those of the Calvin cycle, such as photorespiration. By contrast in water-stressed plants, under both I, J_f (50 and 32 μmol m^{-2} s^{-1}, respectively) exceeded J_c (16 and 0.4 μmol m^{-2} s^{-1}, respectively) showing that processes such as photorespiration can be major sinks for photosynthetic electrons.

Under high I and water limitation, P_N in young leaves was dramatically inhibited (Table 3) and q_P values were very low (Fig. 4). In these leaves, participation of energy-dissipating mechanisms could not entirely compensate for the lack of photosynthetic electron utilisation by CO_2 assimilation. Thus, young leaves of plants whose water supply is limited are solely adapted to low I, since under high I, P_N is inhibited, and they display a high potential for over-reduction of PS2 and thus for photoinhibition.

The drought resistance strategy of cassava is complex. The avoidance mechanisms leading to reduced water loss are associated with heliotropism and drooping. This allows the leaves to moderate the interception of photons when I is high (El-Sharkawy and Cock 1984). Under these conditions, young leaves achieve reasonable P_N while mature leaves are almost totally photosynthetically inactive. When young leaves are forced to intercept high I, they have neither the ability to perform carbon assimilation nor the capacity to dissipate surplus photons. Thus, the strong heliotropic response and drooping of cassava young leaves must be seen as a photoprotective strategy.

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