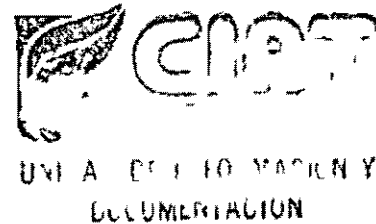


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**Influence of drought in the relationships between the
cassava mealybug and its host plant**

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Executive summary

1- During drought the avoidance mechanisms leading to reduced water loss in cassava are associated with heliotropism and drooping

1 Pendant la secheresse les mecanismes d'evitement de perte d'eau chez la manioc sont associes a helio tropisme et a la posture tombante des feuilles

2- Under water deficiency, young leaves achieve a reasonable rate of photosynthesis which is likely to be of primary importance in acclimation to drought since old leaves are almost totally photosynthetically inactive

2 Pendant un deficit hydrique les jeunes feuilles presentent une activite photosynthetique correcte ce qui semble être de premiere importance pour la plante lors de son acclimatation a la secheresse alors que les vieilles feuilles sont presque photosynthetiquement inactives

3- Higher levels of carbohydrates, free amino acids and organic acids found in leaves of water starved plants contribute to a decrease in the osmotic potential of the tissues in order to protect cellular structure

3 Les plus fortes teneurs en carbohydrates en acides amines libres et en acides organiques rencontrees dans les feuilles de plante en deficit hydrique contribuent a l'abaissement du potentiel osmotique des tissus afin de proteger les structures cellulaires

4- Water stress of cassava plants has a positive effect on the development and reproduction of *P. herreni*. Drought-stressed plants are physiologically more suitable for mealybugs because plant nutrients are more concentrated and better balanced

4 Le stress hydrique chez le manioc a un effet positif sur le developpement et la reproduction de P herreni. Les plantes stressees sont physiologiquement plus convenables aux cochenilles parce que les nutriments y sont plus concentres et mieux equilibres

5- Water stress of cassava plants has a negative influence on the success of parasitism regardless of the parasitoid species used in biological control of *P. herreni* and on the size of progeny depending on the parasitoid species

5 Le stress hydrique chez le manioc a un effet negatif sur le succes de parasitisme independamment de l'espece de parasitoïdes utilisee en lutte biologique contre P herreni et sur la taille des descendants selon l'espece de parasitoïde

6- Recommendation In drought-stricken areas the use of *A. coccois* as biological agent to control *P. herreni* population is recommended. The culture of drought tolerant cassava genotypes should not influence the biological control.

6 Recommandation Dans les zones de secheresse, l'utilisation de A. coccois comme agent de lutte biologique pour contrôler la population de P. herreni est recommandée. La culture de genotypes de manioc tolerants a la secheresse ne devrait pas influencer le contrôle biologique.

General Introduction

The purpose of this report is to mention the main results obtained in the collaborative IRD-CIAT project entitled 'influence of drought in the relationships between the cassava mealybug and its host plant'.

In South America (especially in Northeast Brazil), the cassava mealybug *Phenacoccus herreni* Cox & Williams (Hemiptera: Pseudococcidae) is an important pest of cassava *Manihot esculenta* Crantz (Euphorbiaceae) particularly during drought periods when the insect population increases (Bellotti *et al.* 1983; Noronha, 1990). To control this mealybug, three encyrtid parasitoids *Apoanagyrus (Epidinocarsis) diversicornis* Howard, *Aenasius vexans* Kerrich and *Acerophagus coccois* Smith (Hymenoptera: Encyrtidae) are being studied at the International Centre for Tropical Agriculture (CIAT), Cali, Colombia. They were released in semi-arid areas of the Brazilian states Bahia and Pernambuco in 1994 and 1995 (Smith & Bellotti, 1996; Bertschy, 1998). Despite the presence of cassava mealybug parasitoids, increases in pest populations on cassava are often reported during long dry seasons (A. C. Bellotti and W. M. G. Fukuda, personal observations). These increases could be due to biochemical changes in the cassava leaves induced by water deficiency, resulting in a positive effect on pest development and a negative effect on parasitoid development and/or their searching behaviour.

Therefore, our project was focused on the importance of drought tolerance mechanisms and the changes they might trigger in plant physiology or biochemistry, and what changes this might trigger in mealybug development and in the success of parasitism of three parasitoids and their development.

Part I

Photosynthesis in drought-adapted cassava

Introduction

Because of the essential role of water in plant metabolism plant growth is often proportional to water availability. A prolonged period of severe drought may result in tissue dehydration and death. However, even in the absence of severe water shortage frequent variation in both environmental water availability and water requirements cause regular and transitory water shortage in plants. Those species well-suited to very dry habitats develop special and very effective strategies (short seasonal cycles, CAM metabolism or dehydration tolerance) (Chapin 1993). Most plants react to water deficiency by a range of physiological and morphological adaptations. Short and medium-term acclimation is primarily based on physiological responses leading to reduced water loss (stomatal closure) and utilisation (depressed cell expansion). Long-term acclimation involves anatomical modifications to reduce transpiration and maintain water acquisition (mainly the reduction of the evaporative surface and increased root development) (Davies and Zhang, 1991; Delaunay and Verma 1993).

A lower rate of net CO₂ assimilation in plants suffering from water stress has been often reported (Kaiser, 1987). Both stomatal and non-stomatal factors are thought to contribute to the effects of drought on CO₂ assimilation. Recently published results tend to indicate that 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). Stomatal behaviour is crucial because changes in stomatal aperture affect water loss proportionally more than CO₂ fixation hence improving water use efficiency (WUE) (Martin and Ruiz-Torres, 1992, Gimenez *et al* 1992).

Cassava *Manihot esculenta* 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 orients its leaves in such a way that they seek maximum light interception when the vapour pressure deficit (VPD) is small and solar radiation is low. However they intercept less light at midday when the VPD and solar radiation 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, 1992b, 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 (qP) and the nonphotochemical quenching (qNP). The qP is due to the operation of the photosynthetic electron transport. The qNP arises from nonradiative dissipative processes which function in the regulation of the photosystem II (PSII) photochemistry. These processes compete effectively with the excitation energy transfer processes in PSII, leading to reduced quantum yield but allowing PSII 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, qNP has been shown to dissipate the excess of energy in leaves experiencing various stresses, but the mechanism is not general and differs among species, and according to the type of stress and the adaptation of the plant (Genty *et al.* 1987, Khamis *et al.* 1990, Ogren 1990, Baker 1991, Scheuermann *et al.*, 1991, Jefferies 1994).

In the present study the effect of water stress on photosynthesis 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 irradiance, one may assume that the photosynthetic apparatus in such leaves is not adapted to strong light intensity. Another objective of the study was therefore to examine the susceptibility of PSII to high light through its activity estimated *in vivo* from Chl a fluorescence measurements.

Results

Shoot development was markedly affected by 45 days of water deficiency (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 the leaves that emerged and expanded during the drought period was about half that of the control. All these modifications led to a strongly reduced leaf canopy and correspond to an adaptive reaction of cassava to alleviate water stress. These data 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.* 1992a, El-Sharkawy 1993 and our own observations in the Congo ORSTOM Centre Brazzaville during the dry season). This demonstrates that our experimental conditions mimic field conditions well.

The exposure of plants to water stress did not result in a significant decrease in water potential in either young or old 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, data not shown). Water limitation slightly decreased WC and RWC in young leaves

Table 1 Shoot characteristics of 4-month-old cassava plants grown with high or low water availability for 45 days. 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. Data are means \pm SE.

Treatment	Fallen leaves	Emerged leaves	Area of mature leaves	Height of stem
			cm ²	cm
Control	6 \pm 0.9	12 \pm 0.9	129 \pm 7.6	141 \pm 2.2
Stress	13 \pm 0.9	5 \pm 0.4	66 \pm 8.0	97 \pm 2.2

Table 2 Leaf water status measured before dawn and at midday in young and old leaves of control or water-stressed cassava plants. Data are means \pm SE. WC: water content (g/g dry weight), RWC: relative water content and Ψ_L : leaf water potential (bars).

	WC		RWC		Ψ_L	
	Pre-dawn	Mid-day	Pre-dawn	Mid-day	Pre-dawn	Mid-day
Control plants						
Young leaves	5.3 \pm 0.3	4.2 \pm 0.1	0.91 \pm 0.02	0.91 \pm 0.03	-0.6 \pm 0.07	-0.9 \pm 0.10
Mature leaves	3.6 \pm 0.1	3.5 \pm 0.2	0.94 \pm 0.01	0.88 \pm 0.04	-3.2 \pm 0.13	-3.3 \pm 0.34
Stressed plants						
Young leaves	3.9 \pm 0.2	3.7 \pm 0.1	0.87 \pm 0.01	0.86 \pm 0.01	-0.9 \pm 0.16	-0.7 \pm 0.10
Mature leaves	3.8 \pm 0.4	3.5 \pm 0.3	0.95 \pm 0.003	0.90 \pm 0.01	-3.1 \pm 0.20	-2.3 \pm 0.15

whereas no difference in these parameters was observed in old leaves (Table 2) This probably was due to the fact that the stomata of young leaves of water deficient plants were partially open thus allowing net CO₂ assimilation but also water loss (see below)

Figure 1 illustrates the response of photosynthesis (oxygen evolution) to photon flux density for leaf discs with a saturating CO₂ level In control and water stressed plants the young leaves exhibited a higher maximum rate of CO₂ assimilation than old leaves Water stress reduced photosynthesis in young leaves at a high PPFD the rate at 1000 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ being only 75% of that of the control however there were large variations within leaves of the same water treatment The photosynthetic capacity of old leaves was very low and similar in control or stressed plants

Stomatal conductance increased until midday in young leaves of control plants (Figure 2) It was always significantly higher than in old leaves, whose conductance reached a relatively constant value after 3 h during the light period Stomatal conductance was very low under water limitation irrespective of leaf age A small, transitory increase was nevertheless detectable in young leaves at the beginning of the morning

In leaves of control plants under low light intensity (PPFD intercepted respecting the natural orientation of the leaves) the net photosynthesis (P_n) was almost 5 times higher in young leaves than in old leaves (Table 3) Under water deficit P_n decreased by 66% in young leaves and by more than 90% in old leaves Thus P_n was greater in the young leaves of plants under stress than in old leaves of plants with no stress P_n was greater (about two-fold) in both types of leaves of control plants at high (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) than at low irradiance In contrast P_n were hardly detectable at high irradiance 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 which was extremely low in control leaves (Table 3)

The relative contributions of photochemical (qP) and non-photochemical (qNP) quenching in determining ϕPSII during the induction of photosynthesis in attached leaves are shown in Figure 3 In young leaves at low irradiance the steady-state values of qP and qNP at the end of the induction period were fairly similar in stressed and control plants and hence the values of the quantum yield of electron transport, ϕPSII were comparable Upon transition from low to high irradiance qNP was higher in steady state in both types of plants The increase in qNP was not modified by drought Values of qP decreased with increased irradiance This is the normal response of qP to increasing irradiance However in control plants the change in light caused a substantial and rapid but transient fall in qP which subsequently partially recovered The decrease was greater in stressed plants and qP did not

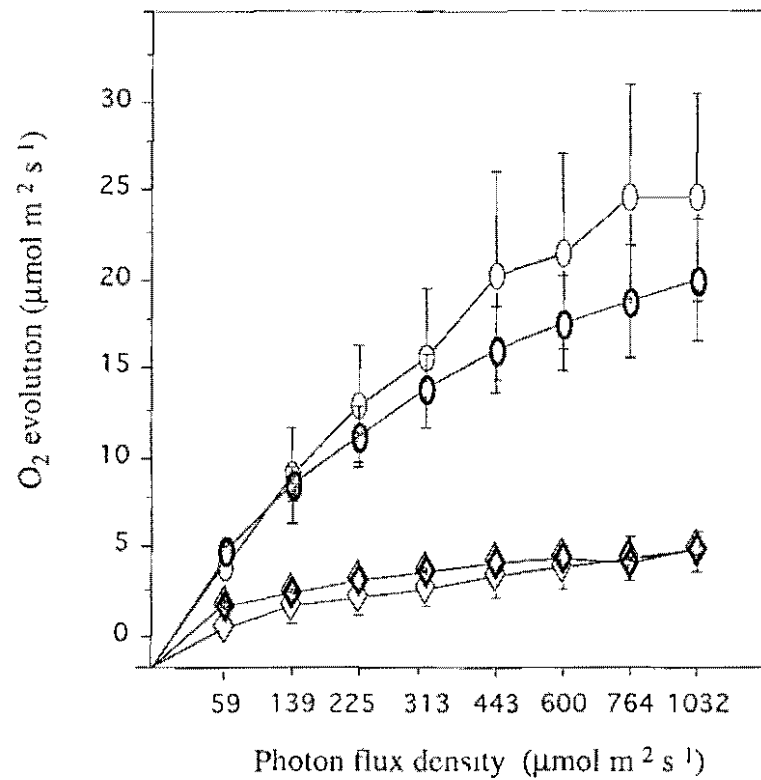


Figure 1 Effect of water limitation on light saturation curves of O_2 evolution in young and old leaves of cassava plants. O_2 evolution was estimated at saturating CO_2 on leaf-discs. Data are means \pm SE.

Symbols: control: \circ young leaves, \diamond old leaves
 stressed: \bullet young leaves, \blacklozenge old leaves

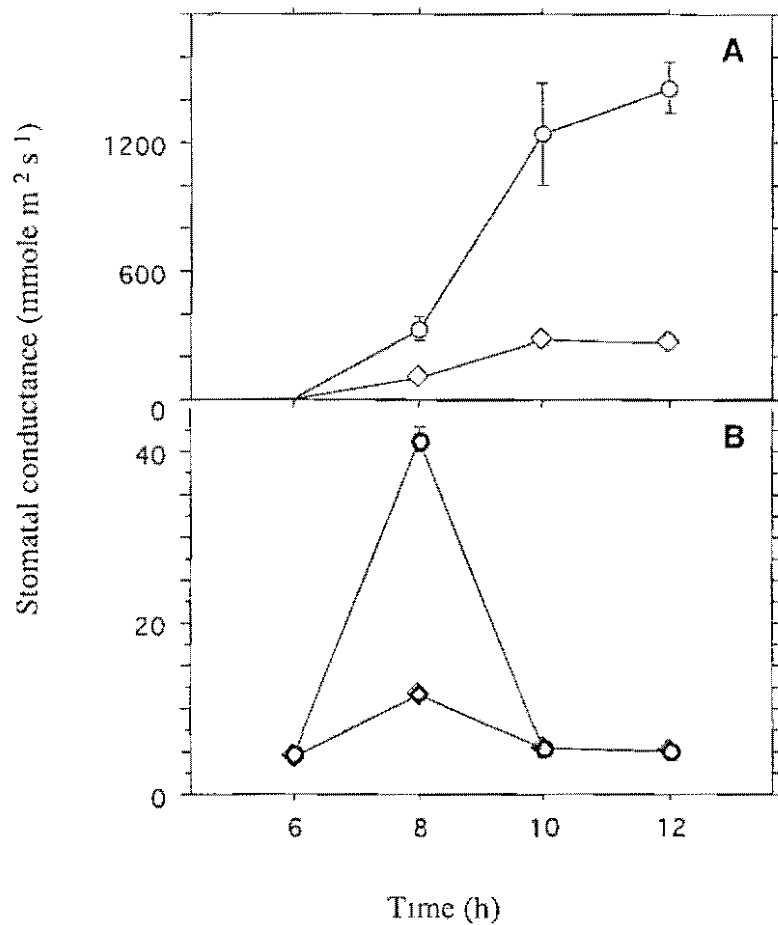


Figure 2 Changes in stomatal conductance of lower leaf surface of young and old leaves of control (A) and water stressed (B) cassava plants from pre-dawn until mid-day. Data are means \pm SE

Symbols control o young leaves, \diamond old leaves
 stressed \circ , young leaves, \blacklozenge old leaves

Table 3 Photosynthesis in normal air chlorophyll contents and *m vitro* phosphoglycolate phosphatase activities of leaves of cassava plants grown under sufficient or limited water availability. Net photosynthesis was determined 4-5 h after dawn at low and high irradiance (PFD of ca 300 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and 1000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ respectively). Measurements were made in young and mature leaves. Data are means \pm SE.

Irradiance	Net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)				Chlorophyll (mg m^{-2})		Phosphoglycolate phosphatase ($\text{nmol (mg Chl)}^{-1} \text{ min}^{-1}$)	
	300 $\mu\text{mol m}^{-2} \text{ s}^{-1}$		1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$		Control	Stress	Control	Stress
	Control	Stress	Control	Stress				
Young leaves	12.2 \pm 0.5	4.0 \pm 0.9	23.9 \pm 0.5	0.1 \pm 0.06	676 \pm 123	617 \pm 44	tr**	337 \pm 146
Mature leaves	2.6 \pm 0.6	0.2 \pm 0.09	4.0 \pm 0.1	nd*	467 \pm 82	454 \pm 114	tr**	218 \pm 25

*nd non detectable tr** traces of activity

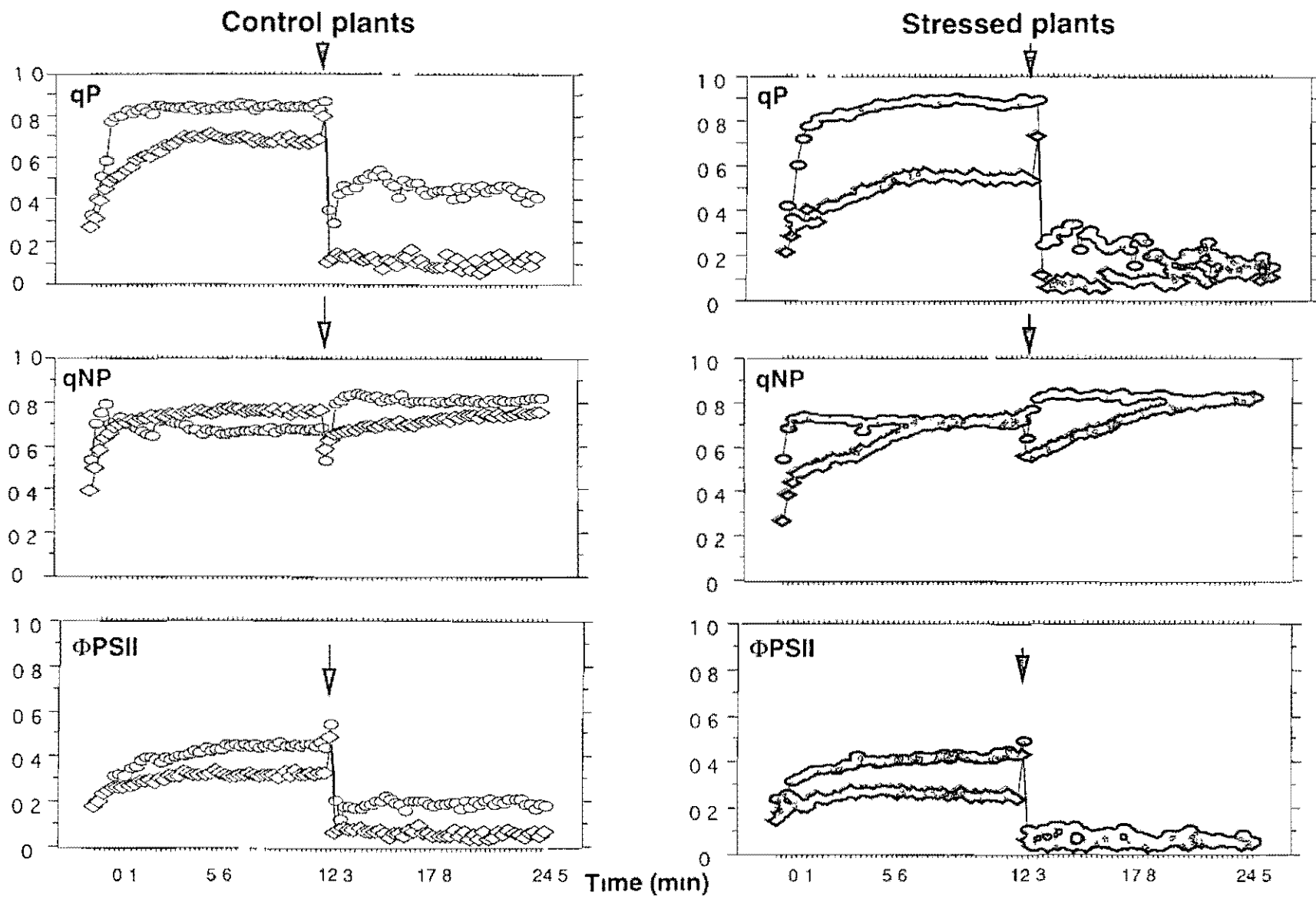


Figure 3 Effect of water deficiency on Chla fluorescence at room temperature. The chemical quenching coefficient (qP), the non-chemical quenching coefficient (qNP) and the quantum efficiency of PSII photochemistry (Φ PSII) were observed during the induction phase of photosynthesis at low irradiance ($220 \mu\text{mol m}^{-2} \text{s}^{-1}$) with a subsequent transition to high ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) irradiance. The experiments were carried out with attached young (o, •) or old (\diamond , \blacklozenge) leaves of stressed (dark symbols) or control (open symbols) cassava plants. Arrows indicate the point of transition in irradiance. Data are means \pm SE.

recover. On the contrary, it continued to fall and reached very low values. Accordingly, at high irradiance in young leaves, ϕ PSII was severely affected as a result of water stress.

Chl a fluorescence analysis revealed substantial differences between old and young leaves. The steady state values reached by qP and ϕ PSII in the control plants at low irradiance were lower in old leaves than in young leaves. Water deficiency depressed these parameters further in old leaves. At high irradiance in old leaves, qP and ϕ PSII were very low in both control and stressed plants.

Discussion

Both the photosynthetic capacity at saturated CO $_2$ (Figure 1) and Pn in normal air found in old leaves (Table 3) are unusual since data obtained by other studies on cassava grown outdoor in pots or in the field showed that similar age of leaves indeed have highest rates of photosynthetic capacity at saturated CO $_2$ and Pn (El-Sharkawy pers. com.). These low rates in our experiments could be due to the shade effect in the glasshouse where the plants were grown. In fact, our study was made under a solar irradiance inferior to 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ which was quite low compared to the experimental conditions used by El-Sharkawy *et al.* (1992b) with a solar irradiance of 1200 to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. However, it is well known in cassava that old leaves displayed lower rates of these parameters than young leaves (El-Sharkawy pers. com., De Tafur *et al.*, 1997).

The old leaves of plants grown with sufficient water supply appeared to have a weak capacity for the utilization of absorbed light. Indeed, the response of old leaves to increasing irradiance in an atmosphere saturated in CO $_2$ clearly shows that the photosynthetic apparatus of these leaves was not effective. At low light intensity in air, their photosynthetic activity was low and fluorescence analysis revealed ineffective PSII photochemistry with relatively low qP and ϕ PSII values. Under high irradiance, CO $_2$ assimilation by old leaves was increased and they displayed very low qP and ϕ PSII values. The low qP values were probably due to insufficient photosynthetic electron utilisation and energy dissipation (Krall and Edwards, 1992). This means that the primary electron acceptor of PSII, QA, was strongly reduced in old leaves under strong light.

In contrast with old leaves, young leaves of control plants exhibited high levels of photosynthetic activities under both saturating CO $_2$ and in air. These leaves also displayed fluorescence parameters usually observed with healthy leaves both under low and high PPFD. Indeed, following a transition from low to high irradiance, they displayed normal behaviour with enhanced Pn and qNP values, allowing qP to remain relatively high and preventing excessive accumulation of light-generated reductant. Nevertheless, the rate in photosynthesis in combination with the leaf area determined carbon uptake. Owing to the respective

proportions of the two types of leaves (old and young) overall photosynthesis in well-watered plants was mainly accounted for by CO₂ assimilation in old 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 old) 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). However, some CO₂ uptake was maintained only in the young leaves under low light intensity whereas Pn in old leaves was almost nil. This probably resulted from stomatal factors (see Figure 2) since the photosynthetic capacity of the old leaves (CO₂ saturated photosynthesis) was not greatly affected by water shortage. Thus, in water-deprived plants both the acceleration of the shedding of old leaves and the pronounced decrease in the photosynthetic activity of these leaves mean that most of the carbon nutrition of the plant as a whole had to be provided by the young leaves. These leaves clearly play a central role in the adaptation of cassava to the stressful environment.

It has been suggested that the photosynthetic capacity is normally 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). The photosynthetic capacity of young leaves of water-deficient cassava plants was decreased by 25% despite their relatively high RWC. Photoinhibition can affect the rate of light saturated photosynthesis (Long *et al.* 1994). A decrease in the ratio of the variable to the maximal fluorescence (F_v'/F_m i.e. $(F_m - F_o)/F_m$) is regarded as showing that the leaf has been photoinhibited (Bjorkman and Powles 1984, Long *et al.* 1994). Our measurements of the F_v'/F_m ratio showed that photoinhibition could not mainly account for the decreased capacity of these leaves as compared to the control (F_v'/F_m was about 0.5 for both types of plants). The decreased photosynthetic capacity of young leaves may have resulted from a reduction in the Calvin cycle capacity as has been reported in some species under water stress (Ogren, 1988, Martin and Ruiz-Torres 1992, Gimenez *et al.* 1992). However, in spite of this decrease, the capability of the photosynthetic machinery remained largely in excess of that required to support the observed photosynthetic rates (Figure 1 and Table 3) and the decrease in Pn observed in young leaves following water shortage resulted mainly from their very low stomatal conductance to CO₂ (Figure 2).

Young leaves displayed consistent but reduced Pn under water stress and low light. No significant difference between stress and non-stress conditions was detected in the Chl_a

fluorescence parameters (Figure 3) That the reduction in Pn did not notably influence qP and ϕ PSII may result from an increase in the rate of reactions (other than those of the Calvin cycle) which consume photosynthetically generated electrons Photorespiration and the reassimilation of the resultant CO₂ is assumed to drain off electrons, 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) Interestingly in cassava leaves, 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) an enzyme that is involved in hydrolysis of the phosphoglycolate formed by RuBP oxygenation which initiates the photorespiratory pathway Furthermore, the extremely low values of phosphoglycolate phosphatase activity in control leaves are not surprising because it is well known that cassava leaves have low photorespiration under well watering conditions (El-Sharkawy and Cock 1990, El-Sharkawy *et al* 1992b)

Under high irradiance and water limitation the photosynthetic activity of young leaves was dramatically inhibited (Table 3) and PSII activity was markedly affected (Figure 3) This is shown by the very low values of qP and ϕ PSII It thus appears that young leaves of plants whose water supply is limited are solely adapted to low light intensity In these leaves it appears that participation of energy-dissipating mechanisms such as photorespiration Mehler type reaction and other could not compensate for the lack of photosynthetic electrons utilisation by CO₂ assimilation under high irradiance and normal air Simultaneously, the capacity for excitation energy dissipation in PSII was not sufficiently increased to allow QA to remain oxidised The maximum value of qNP in C₃ plants is about 0.8 (Weis and Berry, 1987) That qNP had already reached this value in the control plants might explain why it did not further increase with water stress Under high irradiance and normal air their photosynthetic activity is inhibited and they display a high potential for over-reduction of PSII 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 light when irradiance is high (El-Sharkawy and Cock 1984) Under these conditions, young leaves achieve a reasonable rate of photosynthesis which is likely to be of primary importance in acclimation to drought since old leaves are almost totally photosynthetically inactive It appears from the present data that young leaves have neither the ability to use high irradiance for carbon assimilation due to stomatal limitation nor the capacity to dissipate surplus light energy under water stress Thus the strong heliotropic response and drooping of cassava leaves must be seen as a photoprotective strategy necessary to prevent inhibition of photosynthesis and light stress

Part II

Estimation of carbon and nitrogen modification during water deficiency in leaves of *manihot esculenta crantz*

Introduction

In early work cassava was classified as a C3-C4 intermediate (El-Sharkawy & Cock 1987) Later it was demonstrated that the plant displayed C3 photosynthesis (Edwards *et al* 1990) Nevertheless leaves of *Manihot* species have distinct green bundle sheath cells which are unusual in C3 leaves and they show particular photosynthesis characteristics (Angelov *et al* 1993) It could be possible that during water deficiency cassava photosynthesis change from C3 into C4

This study is focused on some changes in C and N metabolisms that water limitation may trigger in cassava leaves

Results and discussion

C concentration in dry mater was not affected by the water availability (Table 4) For both genotypes the $\delta^{13}\text{C}$ values were higher in young leaves as compared to old leaves All these values were increased under water limitation It is well known that stomatal conductance influences $\delta^{13}\text{C}$ since stomata aperture reduces discrimination against ^{13}C during CO_2 fixation Thus, the positive effects of drought on $\delta^{13}\text{C}$ in leaves could result from the lowest conductance of these organs in water limited plants In addition the high $\delta^{13}\text{C}$ values in young leaves of drought-adapted cassava plants was associated with a high PEP Case activity (Table 6) The later enzyme expresses a low isotope fractionation Since young leaves exhibited higher stomatal conductance than old leaves in water limited plants the high $\delta^{13}\text{C}$ values in young leaves could also result from intensive carbon fixation through PEP Case activity However in control plants $\delta^{13}\text{C}$ was higher in young leaves as compared with old leaves PEP Case activity was not different suggesting some stomatal effect in relation to the rate of CO_2 fixation by the photoreductive cycle

For both genotypes and leaf ages, the $\delta^{15}\text{N}$ values were lower but the N concentration in dry mater was slightly higher under low water availability (Table 4) This was associated with higher free amino acid level in stressed plants (Table 5) Serine glutamic acid, glutamine and arginine reached very high levels The amino acid composition was also affected showing a decrease in aspartic acid glutamic acid and alanine proportion and an increase in that of asparagine and arginine (Figure 4)

Table 4 Natural isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and proportions of carbon and nitrogen of young and old leaves of two cassava varieties (CM 1585-13 and CM 507-37) grown under sufficient (NS) or limited (S) water availability (mean from five leaves)

Variety	Treatment	Age of leaves	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N
CM 1585-13	NS	Young	-28.2	2.9	51.0	5.4
		Old	31.0	4.0	51.0	3.0
	S	Young	-24.2	1.8	51.4	5.8
		Old	-26.5	2.2	50.9	4.2
CM 507-37	NS	Young	-29.7	4.2	51.0	5.8
		Old	-30.1	4.0	48.1	3.5
	S	Young	-24.6	2.6	49.6	6.1
		Old	-28.1	2.5	51.6	4.6

Table 5 Free amino acid contents (expressed in nmol/mg Chl) of young and old leaves of two cassava varieties (CM 1585-13 and CM 507-37) grown under sufficient (NS) or limited (S) water availability (mean from five leaves)

	CM 1585-13				CM 507-37			
	NS		S		NS		S	
	Young	Old	Young	Old	Young	Old	Young	Old
Asp	102.8	63.5	143.6	80.2	118.2	39.3	124.2	75.1
Thr	39.8	21.4	63.7	51.2	40.2	21.7	78.5	26.9
Ser	98.4	39.9	203.4	94.5	95.8	33.8	263.3	60.6
Asn	15.4	nd*	114.0	46.2	67.8	20.7	351.5	152.5
Glu	182.6	148.8	282.7	315.7	189.8	135.8	293.0	254.4
Gln	62.9	14.3	226.0	83.9	97.1	15.6	205.9	72.9
Pro	5.3	2.5	10.4	13.4	4.0	2.5	10.8	11.3
Gly	17.2	18.9	31.4	76.9	9.4	5.9	33.6	37.1
Ala	79.0	41.6	109.6	74.6	91.2	55.8	116.5	44.3
Val	10.8	6.3	48.4	25.6	8.8	6.2	48.2	17.1
Cys	18.9	12.8	34.0	32.6	23.0	8.8	35.9	30.9
Met	0.8	nd*	nd*	2.4	0.6	0.1	3.0	1.8
Ile	1.4	2.4	8.3	8.5	1.3	1.5	13.9	8.6
Leu	1.4	1.0	8.1	8.9	1.4	0.9	13.0	9.8
Tyr	1.9	1.0	7.4	22.4	2.1	0.9	12.2	8.8
Phe	5.5	3.2	10.7	12.3	5.6	2.9	10.8	13.9
Lys	2.3	3.0	12.3	7.9	2.6	3.1	16.5	6.9
His	50.6	0.8	21.4	29.5	29.4	1.9	34.3	23.9
Arg	183.6	1.2	474.2	56.4	5.2	0.9	734.4	220.8
Total	880.6	382.6	1809.6	1043.1	793.5	358.3	2399.2	1077.6

*nd not determined

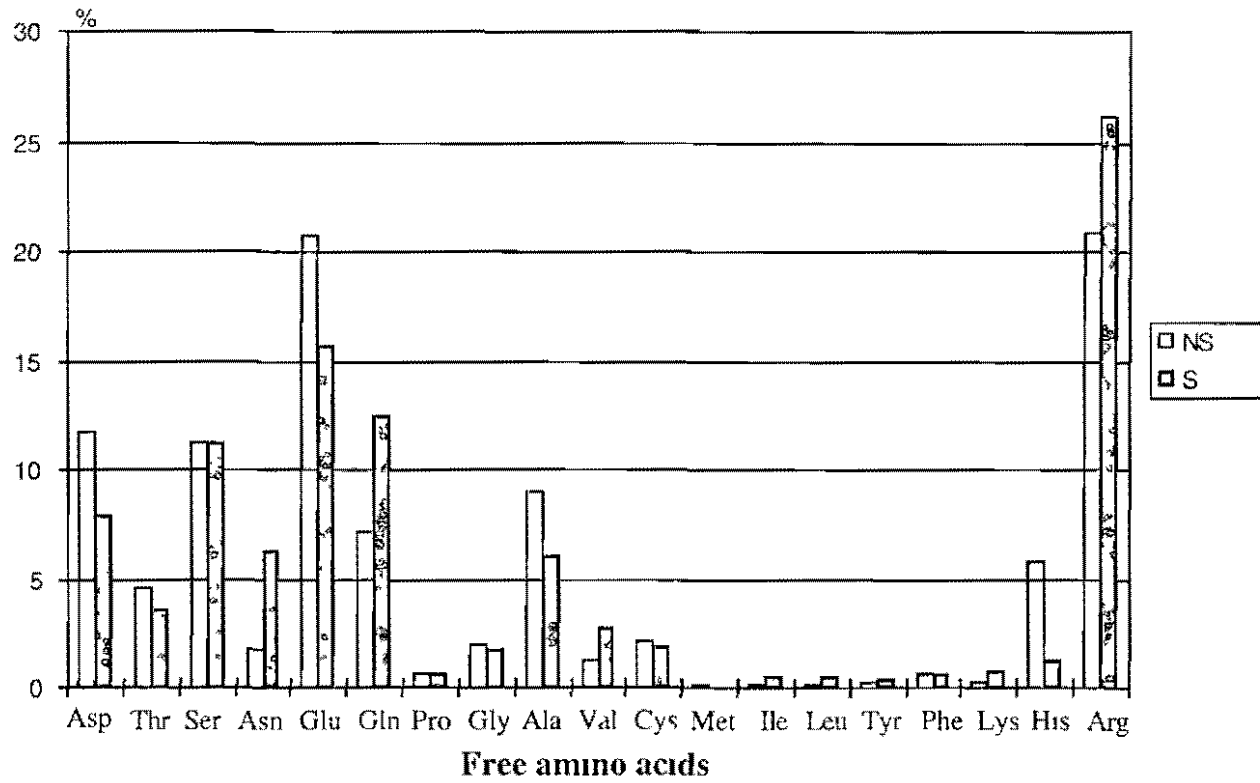


Figure 4 Typical changes of free aminoacids composition of cassava leaves induced by soil water availability (sufficient (NS) and limited (S) water availability)

Table 6 Phosphoenolpyruvate carboxylase (PEP Case expressed in $\mu\text{mol (mg Chl)}^{-1} \text{min}^{-1}$) sucrose phosphate synthase (SPS expressed in $\text{nmol (mg Chl)}^{-1} \text{min}^{-1}$) and phosphoglycolate phosphatase (PGP expressed in $\text{nmol (mg Chl)}^{-1} \text{min}^{-1}$) activities of young and old leaves of two cassava varieties (CM 1585-13 and CM 507-37) grown under sufficient (NS) or limited (S) water availability (mean from five leaves)

	CM 1585-13				CM 507-37			
	NS Young	Old	S Young	Old	NS Young	Old	S Young	Old
PEP Case	0.4	0.7	4.4	0.8	0.8	0.3	5.6	2.4
SPS								
V _{max}	41.0	14.3	26.7	26.5	23.3	10.9	82.4	30.3
V _{lim}	9.3	6.5	15.7	5.9	8.7	4.3	9.4	6.3
PGP	tr*	tr*	168.1	3.7	tr*	tr*	358.2	68.0

*tr traces of activity

Glucose, fructose and sucrose showed modifications of their accumulation levels but the total amount of the three carbohydrates increased following water limitation (data not shown) This was associated with higher sucrose phosphate synthase activity (both maximal and limited activity, Table 6)

Phosphoglycolate amount in leaves was depressed under water limitation (data not shown) This was associated with higher phosphoglycolate phosphatase activity suggesting higher photorespiration (Table 6) An increase in malate succinate and citrate levels was also observed in leaves of water depressed plants (data not shown) This was associated with higher PEP case activity (Table 6)

The higher levels of carbohydrates free amino acids and organic acids found in leaves of water starved plants contribute to a decrease in the osmotic potential of the tissues in order to protect cellular structures Furthermore there is no evidence that cassava display a C3-C4 intermediate photosynthesis or change its photosynthesis into C4 during water shortage An alternative hypothesis is that the high phosphoenolpyruvate carboxylase activity found under water limitation is due to an increase in photorespiration leading to an acceleration of respiratory ammonium assimilation requiring a high anapleuretic phosphoenolpyruvate carboxylase functioning

Part III

Influence of cassava plants under water stress on the cassava mealybug and three parasitoid species

Introduction

Mattson & Haack (1987) reported that drought-stressed plants are often more suitable for insect growth and reproduction because plant nutrients are either more concentrated or better balanced. Thus increasing and/or improving the balance of these nutrients should favour insect performance explaining in part the often-reported outbreaks of plant-eating insects on drought-stressed plants. In Africa, for example, increases in pest populations are often observed on cassava plants during long dry seasons with another cassava mealybug species *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae) (Neuenschwander *et al.* 1990, Le Ru *et al.* 1991). Under laboratory conditions Fabres & Le Ru (1988) showed that *P. manihoti* exhibited a higher intrinsic rate of increase (r_c) on cassava plants under water stress, inducing an increase in the *P. manihoti* population.

The natural enemies of phytophagous insects function and develop in a multitrophic context (Price *et al.* 1980). Consequently their behaviour and physiology, which determine their fitness, are influenced by many factors and stimuli derived from the plant (first trophic level) and the phytophagous host (second trophic level) (Vinson 1976, Takabayashi *et al.* 1991). A great number of studies have focused on the interactions between plants and pests (Maxwell & Jennings 1980) and between pests and parasitoids (Waage & Hassell 1982). In recent years a common theme of integrated control has been to combine the selection of plant variety with biological control therefore it has been necessary to study the influence of plants on interactions between herbivorous insect pests and their parasitoids (Van Emden 1987, Souissi & Le Ru, 1998). The plant influences host habitat location, host searching by the natural enemy and the oviposition behaviour of parasitoids. It acts either directly via its physical and chemical characteristics or indirectly by means of chemical cues derived from host (honeydew) activity or nutrition (Vet & Dicke, 1992, Godfray, 1994). It also affects the survival of the parasitoid until adult stage thereby influencing its size, fecundity and developmental time (Reed *et al.*, 1991, Souissi & Le Ru 1998). In order to estimate the parasitoid's efficiency in biological control, it is thus necessary to consider the first trophic level (Tingle & Copland 1988, Van Emden 1991, Souissi & Le Ru, 1998).

Mattson & Haack (1987) emphasized that drought provokes outbreaks of leaf-eating insects by providing nutritional conditions that favour their growth and immunocompetence. These changes also favour the insect's escape from regulation by their natural enemies. Under laboratory conditions the parasitoid *Apoanagyrus lopezi* De Santis (Hymenoptera

Encyrtidae) released in Africa to control *P. manihoti* exhibits a lower preference for parasitizing mealybugs reared on cassava plants under water stress (B. Le Ru, personal communication). Furthermore, Souissi & Le Ru (1998) showed that cassava genotype influences the development of this parasitoid species. In the system under study, it is necessary to understand the drought-tolerance mechanisms of cassava, the changes they might trigger in plant physiology and biochemistry, and what effect these changes have on the mealybug and its parasitoids.

The purpose of this study was to evaluate the influence of cassava plants under induced water stress on *P. herreni* development and on the success of parasitism of three parasitoids and their development. The parasitoid species studied were *A. diversicornis*, *A. vexans*, and *A. coccois*. The use of the cassava genotype (more or less drought tolerant) and parasitoid species most suitable for controlling *P. herreni* in dry areas is discussed.

Results

Development time of females to ovisac formation was significantly lower on both genotypes when *P. herreni* was reared on water-deficient plants (Table 7). In contrast, female fecundity was higher. On CM 507-37, a similar tendency was observed for female fecundity; thus, no statistical significance was obtained.

For both cassava genotypes, the weight of mature females and the intrinsic rate of increase (r_m) were significantly higher when *P. herreni* was reared on water-stressed cassava plants. Furthermore, the weight of adult females was higher on CM 507-37 regardless of the water treatment.

Sex ratio was influenced more by the genotype than the water treatment. The ratio was about 2.2 and 2.3 (male:female) on CM 507-37 and CMC 40, respectively.

The rate of parasitism was generally lower in mealybugs reared on water-stressed plants (Table 8). In contrast, the death rate was generally higher. No tendency was observed for the emergence and survival rate parameters, which were generally not influenced by the plant's water status.

Furthermore, when statistical significance was noted, the encapsulation rate was higher in mealybugs reared on water-stressed plants and the developmental time was lower.

A comparison among parasitoid species showed that the rate of parasitism of *A. coccois*, regardless of the plant water status and genotype, was generally higher as compared to the rates of *A. vexans* and *A. diversicornis*.

Table 7 Biological characteristics of *P. herroni* females reared on cassava plants grown with sufficient (NS) or limited (S) water availability and results of 2 way ANOVA (genotype and water-treatment factors) when there is homogeneity of variance and data normality. The developmental time (in days) to ovisac formation, the fecundity of mature females (total no. of eggs laid per female), the intrinsic rate of increase (r_m), weight (in mg) and sex ratio (% female) were determined (means \pm SE followed by the no. of replicates in parentheses). For each plant genotype, different letters in the same column (water availability comparison) indicate significance ($P < 0.05$) derived from Student's *t*-test or from Mann-Whitney *U* test for the developmental time to ovisac formation and weight.

Cassava cultivar		Developmental time to ovisac formation	Fecundity	r_m	Female weight	% female
CM 507-37	NS	23.3 \pm 0.05 (88)b	420.2 \pm 40.0 (13)a	0.286 \pm 0.004 (13)a	1.3 \pm 0.03 (88)a	48.1 \pm 1.7 (7)a
	S	22.7 \pm 0.1 (75)a	496.6 \pm 27.9 (9)a	0.300 \pm 0.003 (9)b	1.5 \pm 0.04 (75)b	54.9 \pm 5.8 (6)a
CMC 40	NS	23.3 \pm 0.2 (52)b	394.1 \pm 34.9 (7)a	0.285 \pm 0.004 (7)a	1.1 \pm 0.04 (52)a	62.2 \pm 4.1 (7)a
	S	22.4 \pm 0.05 (92)a	532.5 \pm 39.5 (10)b	0.305 \pm 0.003 (10)b	1.3 \pm 0.03 (92)b	61.1 \pm 3.6 (6)a
ANOVA						
genotype (A)			0.9005	0.6103		0.0171
treatment (B)			0.0095	0.0001		0.4822
A x B			0.4335	0.4098		0.3211

Table 8 Influence of the water treatment of cassava plants on success of parasitism and on development time of three parasitoid species of *P. herreni*. Two cassava cultivars (CM 507 37 and CMC 40) were grown under sufficient (NS) or limited (S) water availability. For each parasitoid species and each cassava cultivar, different letters in the same column (a, b = water availability comparisons) indicate significance ($P < 0.05$) derived from Chi square test or from Mann-Whitney *U* test for developmental time.

Parasitoid	Cassava cultivar		Rate of parasitism (%) ^a	Emergence rate (%)	Encapsulation rate (%)	Survival rate (%)	Death rate (from insertion of ovipositor or direct feeding) (%)	Total no of observed malybugs	Developmental time (in days, mean \pm SE)(n) ^b
<i>A. coccois</i>	CM 507 37	NS	61.7 b v	75.1 a	0	6.4 a	31.9 a	77	20.7 \pm 0.2 (36)a
		S	41.4 a v	74.8 a	0	12.2 a	46.4 b	71	20.3 \pm 0.1 (22)a
	CMC 40	NS	60.8 b v	78.3 a	0	14.2 a	25.0 a	86	20.7 \pm 0.1 (41)a
		S	46.2 a v	80.2 a	0	15.3 a	38.5 b	82	20.2 \pm 0.1 (30)a
<i>A. vexans</i>	CM 507 37	NS	43.7 a u	76.7 a	7.9 a	15.7 a	32.7 a	81	31.6 \pm 0.3 (27)b
		S	32.0 a v	69.5 a	4.0 a	30.0 b	34.0 a	80	23.7 \pm 0.4 (18)a
	CMC 40	NS	59.5 b v	66.6 a	3.7 a	22.0 a	14.8 a	80	23.0 \pm 0.3 (32)b
		S	27.3 a u	67.0 a	14.3 b	14.3 a	44.1 b	82	20.7 \pm 0.1 (15)a
<i>A. diversicornis</i>	CM 507 37	NS	44.4 b u	67.6 a	8.1 a	10.8 a	36.7 a	67	25.7 \pm 0.2 (20)b
		S	25.0 a u	69.4 a	25.0 b	8.3 a	41.7 a	78	22.2 \pm 0.4 (14)a
	CMC 40	NS	40.7 b u	63.9 a	16.7 a	11.6 a	31.0 a	72	25.4 \pm 0.2 (19)b
		S	31.2 a u	69.8 a	13.5 a	9.1 a	46.2 b	82	22.8 \pm 0.6 (18)a

^afor each cassava cultivar and each water treatment, different letters in the same column (u, v = parasitoid species comparisons) indicate significance at 5% level derived from a Chi square test.

^bfor *A. coccois* and *A. vexans*, developmental time for both sexes.

Based on the sex ratio and the size of progeny tibia these parameters were not influenced by the water status of the plants (Table 9). For *A. diversicornis* alone the tibia length and thus progeny size were significantly lower on water-stressed plants.

Discussion

Cassava plants under water stress favour *P. herreni* development and reproduction. In fact the developmental time of females to ovisac formation was shorter, moreover fecundity, the intrinsic rate of increase (r_m) and the weight of mature females were higher (Table 7). These data indicate a faster increase in the number of pests on cassava under low water availability, thereby explaining in part the mealybug outbreak on cassava during long dry seasons observed in the field by Bellotti *et al.* (1983) and Noronha (1990). Furthermore, according to the parameters evaluated in this study (fecundity, r_m , weight of females) the positive effect of water-stressed cassava on *P. herreni* development and reproduction could be related to nutritional factors, as suggested by Mattson and Haack (1987), e.g. plant nutrients are either more concentrated or better balanced. In fact cassava leaves under water deficit exhibit an increased level of some compounds such as free amino acids, carbohydrates (sucrose) and organic acids (malic and succinic) contributing to a decrease in the osmotic potential of the tissues in order to protect cellular structures (see Part II). Using a bio-assay method for mealybugs developed by Calatayud *et al.* (1998), an increase in the level of these compounds in the diet and the use of a molar ratio (sucrose/free amino acids) at 2.5, found in cassava leaves under low water availability (vs 5 for well-irrigated plants) favours *P. herreni* growth (unpublished data, CIAT, 1999). All these observations confirm the fact that under water stress cassava favours *P. herreni* growth and reproduction because plant nutrients are either more concentrated or better balanced (ratio sucrose/free amino acids). Nevertheless, according to our results, there is no evidence that more drought-tolerant cassava genotypes are more favourable to mealybug development and reproduction. The single advantage that CM 507-37 presented as a mealybug host over CMC 40 was the weight of the adult female, which was higher under the same conditions. This does not mean that the use of drought-tolerant cassava to manage mealybug populations should not be recommended because such genotypes should be more tolerant to mealybug infestations, which induce water stress in cassava (Calatayud *et al.* 1994, P.-A. Calatayud, personal observations). Furthermore, according to the results of the sex ratios (Table 7) the more drought-tolerant genotype CM 507-37 appears less favourable to the female population, considered as more responsible for cassava damage by Polania *et al.* (1999).

According to the results obtained with the parasitoids, successful parasitism is influenced by the plant's water status. Water-stressed cassava plants induce a decrease in the

Table 9 Influence of water treatment for cassava plants on tibia length (μm mean \pm SE) and on sex ratio (represented by % females) of three parasitoid species. Two cassava cultivars (CM 507-37 and CMC 40) were grown under sufficient (NS) or limited (S) water availability. For each parasitoid species, different letters in the same column (water-availability comparisons) indicate significance ($P < 0.05$) derived from Mann-Whitney U test. For the percent females, the same letter in a column (water-availability comparisons) indicate no significance ($P > 0.05$) derived from Student's t -test for *A. coccois* or from Chi-square test for *A. vexans*.

Parasitoid	Cassava cultivar		Tibia lengths of male	Tibia lengths of female	% females ^a
<i>A. coccois</i>	CM 507-37	NS	227 \pm 4 a	234 \pm 3 a	70.1 \pm 4.5 a
		S	220 \pm 4 a	235 \pm 2 a	70.4 \pm 3.8 a
	CMC 40	NS	232 \pm 4 a	238 \pm 4 a	81.2 \pm 3.9 a
		S	236 \pm 6 a	239 \pm 3 a	78.0 \pm 3.4 a
<i>A. vexans</i>	CM 507-37	NS	427 \pm 10 a	432 \pm 6 a	71.4 a
		S	419 \pm 23 a	458 \pm 22 a	66.7 a
	CMC 40	NS	421 \pm 15 a	451 \pm 17 a	71.4 a
		S	410 \pm 12 a	468 \pm 11 a	70.0 a
<i>A. diversicornis</i>	CM 507-37	NS	-	618 \pm 15 b	100.0
		S	-	483 \pm 12 a	100.0
	CMC 40	NS	-	608 \pm 20 b	100.0
		S	-	494 \pm 21 a	100.0

^aFor *A. coccois* mean \pm SE

rate of parasitism regardless of the parasitoid species studied (Table 8) but there is no evidence that more drought-tolerant cassava genotypes are less favourable to the success of parasitism. In fact lowest parasitism rates for both genotypes were obtained on water-stressed plants.

During host selection parasitoids use a variety of cues to assess the quality of their hosts such as shape, surface structure and internal and external chemical substances (waxy secretions and honeydew) (Godfray 1994). It is well known that the quality and quantity of these substances vary according to the species, variety and plant resistance level influencing host discrimination by parasitoids (Takabayashi & Takahashi, 1993). At the time of oviposition the quality of parasitoid hosts depends on their age or stage of development, size condition and diet (Godfray, 1994). In this study the experimental conditions, the genotype, host age and stage of development were identical for both cultivars, the diet was the only varying factor. Our data demonstrate that the diet of *P. herreni* influences the parasitism rate of parasitoid species, suggesting that water stress influences host discrimination by the parasitoids. Furthermore, the most appropriate candidate among the parasitoid species studied for biological control in drought-stricken areas could be *A. coccois*. In fact a higher rate of parasitism was obtained with this species on cassava under low water availability (Table 8).

When statistical significance was obtained, higher encapsulation rates were observed with *A. vexans* and *A. diversicornis* when mealybugs were reared on water-stressed cassava plants (Table 8). As already noted by Bertschy (1998) no encapsulation was observed with *A. coccois* species. It is well known that in the ability of the parasitoid to resist the defence mechanisms of the host, all known mechanisms to avoid encapsulation, used—either by the female parasitoid (during oogenesis or oviposition) or by the embryo (formation of lytic cells at the serosal level without intake of exogenous nutrients) (Nenon *et al.*, 1988)—depend upon the species. Furthermore, it has been demonstrated that intensity in the mealybug's immune reaction changes with the age and stage of the host (Sullivan & Neuenschwander 1988; Iziquel 1990): older hosts encapsulate more often than younger ones because they contain more hemocytes. In our experiment, the mealybugs used were at the same age and stage. The higher encapsulation rate recorded on mealybugs reared on water-stressed plants suggests that the trophic characteristics of the plant may influence the intensity of the mealybug's immune reaction and that cassava under water stress could have a positive influence on this. As mentioned by Mattson & Haack (1987) drought enhances the insect immune system.

In contrast, two other parameters (Table 8) are not favourable to mealybugs. The death rate, mainly due to direct feeding by the parasitoid in our experiment (data not shown) was found to be higher in mealybugs reared on water-stressed plants. This could be related to some trophic quality of the host enhanced when the cassava plants are under water stress.

confirming the fact that successful parasitism is related to the host diet. Except for *A. coccois*, the developmental time of parasitoids was found to be lower in mealybugs reared on water-stressed plants. This could be related to the fact that the developmental time of *P. herreni* was lower on cassava under low water availability.

Furthermore, only in the case of *A. diversicornis* tibia length and thus progeny size were reduced on water-stressed plants (Table 9). With the cassava mealybug parasitoid species *Apoanagyrus lopezi*, the number of oocytes contained in the ovarioles of females is positively correlated with body size (Van Dijken *et al.*, 1991). The larger size females live longer and have a greater probability of mating successfully (Kraaijeveld & Van Alphen, 1986). Previous studies showed that female fitness increases with adult size (King, 1988; Visser, 1994). Our results with *A. diversicornis* suggest a lower expression of the fitness on cassava under water-deficit conditions.

As Kraaijeveld & Van Alphen (1986) have emphasized with *A. lopezi*, our parasitoid species are koinobiont parasitoids, whose larvae develop in a host that continues to feed and grow after having been parasitised. Contrary to idiobiont parasitoids, the size of the imago may be related to the growth of the host (Waage, 1982). For *A. diversicornis*, smaller adults were obtained on cassava under water deficit conditions (Table 9) whereas larger mealybugs were obtained on these same plants (Table 7). These data indicate that the ability to regulate parasitoid growth is expressed differently according to the water status of the host plant. This observation, which is valid only for the asexual strain used in this study, suggests that progeny size of this reproduction type should be more sensitive to the first trophic level. In the future, therefore, consideration of the type of parasitoid reproduction should be useful in the biological control of *P. herreni* in drought-stricken areas.

In conclusion, we showed that water stress of cassava plants has a positive effect on the development and reproduction of *P. herreni* females and a negative influence on both the success of parasitism, regardless of the parasitoid species, and on the size of parasitoid progeny, depending on the parasitoid species, explaining in part the increase in mealybug populations on cassavas during long dry seasons. As mentioned by Mattson & Haack (1987), while drought-stressed plants are physiologically more suitable for phytophagous insects because plant nutrients are either more concentrated or better balanced, simultaneous drought disfavours natural enemies of phytophagous insects. Furthermore, in drought-stricken areas, more drought-tolerant cassava genotypes should not be less favourable for controlling *P. herreni* populations, and *A. coccois* would be most appropriate among the parasitoid species studied.

General conclusion

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 light when irradiance is high. Under these conditions young leaves achieve a reasonable rate of photosynthesis which is likely to be of primary importance in acclimation to drought since old leaves are almost totally photosynthetically inactive. It appears that young leaves have neither the ability to use high irradiance for carbon assimilation due to stomatal limitation nor the capacity to dissipate surplus light energy under water stress. Thus, the strong heliotropic response and drooping of cassava leaves must be seen as a photoprotective strategy necessary to prevent inhibition of photosynthesis and light stress.

There is no evidence that cassava displays a C3-C4 intermediate metabolism or change from C3 to C4 under water shortage. The higher levels of carbohydrates, free amino acids and organic acids found in leaves of water starved plants contribute to decrease the osmotic potential of plant cells to preserve cellular structure. The high phosphoenolpyruvate carboxylase activity found under water limitation could be due to an increase in photorespiration leading to an acceleration of respiratory ammonium assimilation requiring a high anapleuretic phosphoenolpyruvate carboxylase functioning.

Furthermore, water stress of cassava plants has a positive effect on the development and reproduction of *P. herreni* females and a negative influence on both the success of parasitism regardless of the parasitoid species, and on the size of parasitoid progeny, depending on the parasitoid species explaining in part the increase in mealybug populations on cassavas during long dry seasons. In fact while drought-stressed plants are physiologically more suitable for phytophagous insects because plant nutrients are either more concentrated or better balanced, simultaneous drought disfavours natural enemies of phytophagous insects. Furthermore in drought-stricken areas more drought-tolerant cassava genotypes should not be less favourable for controlling *P. herreni* populations, and *A. coccois* would be most appropriate among the parasitoid species studied.

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CALATAYUD P -A M A POLANIA C D SELIGMANN AND A C BELLOTTI 2000 Influence of cassava plants under water stress on the cassava mealybug and three parasitoid species **Submitted** to Bulletin of Entomological Research

Team performance

The work of M A Polania entitled 'Feeding behaviour of the mealybug *Phenacoccus herreni* (Sternorrhyncha Pseudococcidae) and influence of water deficiency in cassava plants on its development' was selected in the XXI Congress of the Colombian Entomological Society (SOCOLEN) for the best scientific work presented by students in 1998. She received at 18 July 1999 the first "Francisco Gallego" prize. M A Polania from the Javeriana University of Bogota was student in the project during 1998.