SOME ASPECTS OF RESPONSE TO DROUGHT IN THE GENUS *PACHYRHIZUS* RICH. EX DC.

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ABSTRACT

The responses in leaf water relations and gas exchange were followed in well-watered and water-stressed plants of two genotypes of yam bean (*Pachyrhizus* Rich. ex DC.). Preliminary results with well-irrigated plants showed that EC033 (*Pachyrhizus erosus* (L.) Urban) more efftciently controlled its leaf water loss than AC 102 (*Pachyrhizus ahipa* (Wedd.) Parodi). This control was ensured through its better stomatal regulation which was responsible for a better daily integrated water use efficiency in EC033 (+12%) as compared to those in AC102. Drought did not affect the midday leaf RWC in both cultivars, appreciable effect was observed only after 15 days of drought resulting in a reduction of leaf water potential in AC102. However, a significant osmotic adjustment (- 1.1 MPa) was observed in the leaves of' AC 102 which contributed to the maintenance of a positive leaf turgor. These data dcsignate EC033 as a good drought avoider and AC102 as a drought tolerant cultivar. Although drought caused a reduction in mid-day leaf conductance, photosynthesis, and transpiration there were no significant differences between genotypes with respect to these processes. Rut, at thc scale of thc day EC033 continued to maintain higher RWC and gas exchange activities than AC102. However, under the prevailing dry conditions of this experiment AC102 maintained a lower but more stabilized yield than EC033. These data were the first ever obtained on *Pachyrhizus* and demonstrate that a diversity exists within the genus, and that this can be exploited to identify well adapted materials to semi-arid conditions

INTRODUCTION

The dsvelopment and persistence of drought is one of the most important problems affecting crop and food production on most arable farmlands. This is particularly so in the Sahelian area, extcnding from West to East Africa, between the North of the Sahara desert and the Sudanese climatic area (Bailey, 1979), in which cultivated species today are becoming less adapted to the general reduction and the erratic distribution of rainfall. In this area, and in semi-arid zones in general, one of the major strategies of increasing or stabilising crop production is to increase the level of adaptation to drought of these species. One closely related strategy to the former, poorly exploited at present, is an increase in the inter-specific diversity existing in this area through thc introduction of new species which art' more adapted to thc prevalent climatic and agricultural conditions.

Pachyrhizus Rich ex DC. also commonly called yam bean, is currently being evaluated along these lines in Sénégal (West Africa, Northetn Sahel). *Pachyrhizus* possesses four advantages of equal importance for agricultural systetns in the Sahelian area. Firstly, as a legume it can be cultivated on soils of poor fcrtility, hence contributiny to their regeneration. Secondly, it can contrihute to the food requirements of the population in this area through its high tuber production and quality. Thirdly, vegetative parts can be used as livestock feeds Finally, the seeds of *Pachyrhizus* contain rotenone which can be used as an insecticide for crops (See Adjahossou and Halafiki in this review)

The genus *Pachyrhizus*, originates from Central America, and includes five specics (*P. tuberosus* (Lam.) Spreng, *P. erosus* (L.) Urban, *P. ahipa* (Wedd.) Parodi, *P. ferrugineus* (Piper) Sørensen, and *P. panamensis* Clausen) that have been described by Sørensen (1990) and is cultivatcd in areas where mean annual precipitation ranges between 250 mm and 2000 mm. The introduction of *Pachyrhizus* to the Sahelian area, where mean annual precipitation ranges between 800 mm and sometimes less than 100 mm, must be preceded by a thorough study of its responses to drought, and a subsequent choice of varieties which arc bettcr adapted to the different dry zones. In spite of its agronomic interest, the physiology of the genus has apparently not been studied except for the work conducted at INRA/Guadeloupe (Zinsou *et al.*, 1987 and in this review; Vaillant *et al.* 1990; Robin *et al.*, 1990) on the source/sink relationships of *Pachyrhizus*. At the moment, therefore, no data is available on the performance of *Pachyrhizus* grown under drought conditions The present paper provides information on some responses of *Pachyrhizus* to drought, particularly on leaf water relations, leaf gas exchanges and their relationships aith production. The principal form of agronomic drought in Senegal is terminal drought (Annerose, 1991). This study was conducted to evaluate some responses of *Pachyrhizus* to terminal drought with the objectives of characterising some of the different forms of reaction of the genus in these conditions.

MATERIALS AND METHODS

Plant material and growth conditions

The present experiment was conducted in 1992 at Bambey (Sénégal) at "Centre National de Recherches Agronomiques". *Pachyrhizus erosus* (L.) Urban (EC033) and *Pachyrhizus ahipa* (Wedd.) Parodi (AC 102) plants were grown from seeds in large pots (h = 40 cm. ∅ 25 cm) containing 28 kg of sandy soil. The pots were placed in a greenhouse at a maximum temperature of 35°C' and received natural light with a photon flux density (PFD) superior to 1500 µmoles m-2 s-l at mid-day. Effective and efficient nodulation was induced by treatment of the seeds with *Bradyrhizobium*. The plants were regularly irrigated during the early stages of growth and were thinned to one per pot by the sixth week after planting A t the beginning of pod formation and filling stage (Ri) the plants of each species were divided into two groups of five plants per group. irrigation was withheld for the plants in the stressed group (S) whereas control plants (T) were irrigated.

Measurements

Preliminary measurements of leaf gas exchanges were made 5 days hefore the onset of stress All other measurements were taken every second day during the treatment period.

Leaf gas exchange measurements (photosynthesis and transpiration, P and E) were made with a carbon dioxide leaf chamber analysis system (LCA-3, ADC) coupled to a Parkinson leaf chamber (PLC-3/N, ADC). Measurements were quickly repeated three times on the third or the fourth leaf from the top of each plant. Leaf relative water content (RWC) and leaf water potential (ψf) were measured immediately afterwards. A leaf disc

disc was measured within one hour of collection. After 2 hours of rehydration by submerging in distilled water the turgid weight ('Tw) ofthe sample was measured. The dry weight (Dw) was also recorded after drying for 24 hours at 80°C. The RWC was calculated as RWC = ((Fw-Dw)/(Tw-Dw)) x 100. Another disc punched from the same leaf was quickly placed in a sample chamber (C30, Wescor) connected to a micro voltmeter (PR 55, Wescor) for thermocoupled psychrometric measurement of ψf. The measurements were made 3 hours after equilibration in the laboratory, and the outputs were converted to bars using calibration curves established with NaCl solutions of different osmolalities. Immediately afterwards, the psychrometric chamber and sample assembly were frozen for later determination of leaf osmotic potential (ψos) After thawing ψos was measured directly as previously described for ψf Leaf bulk turgor potential (ψt) was also calculated as the differcnce between ψf and ψos

The plants were harvested 25 days after the start of the water stress treatment. The fresh weight of the tubers and other vegetative parts were immediately measured; the corresponding dry weights were also measured after drying for 24 hours in an oven at 80°C The soil water content in each pot was determined gravimetrically at harvest

RESULTS AVD DISCUSSION

Preliminary study: Gas exchangc in well irrigated conditions

Preliminary results on gas exchange obtained 5 days before the onset of stress are shown in figure 1. With a daily maximum photosynthetic photon flux density (PPFD) value of 1850 μmoles/ m^1/sec^{-1} at 13:00 h the daily maximum photosynthetic rates (P) for AC102 and EC033 were 18.0 and 16.5 ψ moles $CO_2/m^2/sec^{-1}$ obtained respectively at 12:00 and 11:00 h (fig. 1a). The relationship between P and PPFD was established for each variety using a hyperbolic rectangular function, and this suggests that at high PPFD values AC102 had slightly higher maximum leaf photosynthetic rate than EC003 (fig. 1b). Higher daily transpiration rates (E) were observed at 14:00 hours for both varieties but between 11:00 and 16:00 h AC102 maintained a significantly higher E rate than EC033 suggesting a better leaf water loss control by EC033 during the highest daily evaporative demand period (fig. 1c) Daily water use efficiency (WUE) was calculated as P/E. For both varieties WUE decreased between 11:00 and 16:00 h but from 11:00 h EC033 maintained a higher hourly WUE than AC102 resulting from its better control of leaf transpiration (fig. 1d) The total daily WUE was calculated as the integrated surface under each individual curve (fig. Id). In spite of a lower hourly WUE than AC102 before 10:00 h, EC033 exhibited a greater total daily WUE (+ 12%). These gas cxchange values. the first ever obtained on yam bean, agree with those generally found in many leguminous plants growing in non-limited water conditions (Bhagsari et *al.*, 1976; Bunce, 1982; Turner *et al* 1984; Cortes *et al.*, 1986). Nevertheless these values vary substantially among genotypes, thus indicating a better water use regulation by EC033, and suggesting a better level of adaptation of this genotype to well irrigated but hot conditions. These differences in gas exchange values between the two genotypes were most largely experienced at mid-day (fig la. 1c 1d). Subsequent measurements. therefore, were generally conducted at 12:OO h during the water stress treatment. However, in order to better differentiate thc daily responses of the 2 genotypes. measurements were atso taken at 08:00, 12:00 and 17:00 h on specific days.

Fig.1 Hourly changes in leaf (a) photosynthesis, (c) transpiration and (d) water use efficiency, and (b) relationship between photosynthesis and PPFD in *Pachyrhizus*. Measurements were taken 5 days before onset of stress. Vertical lines represent the mean interval of confidence P = 0.05; (■) AC102; (□) EC033.

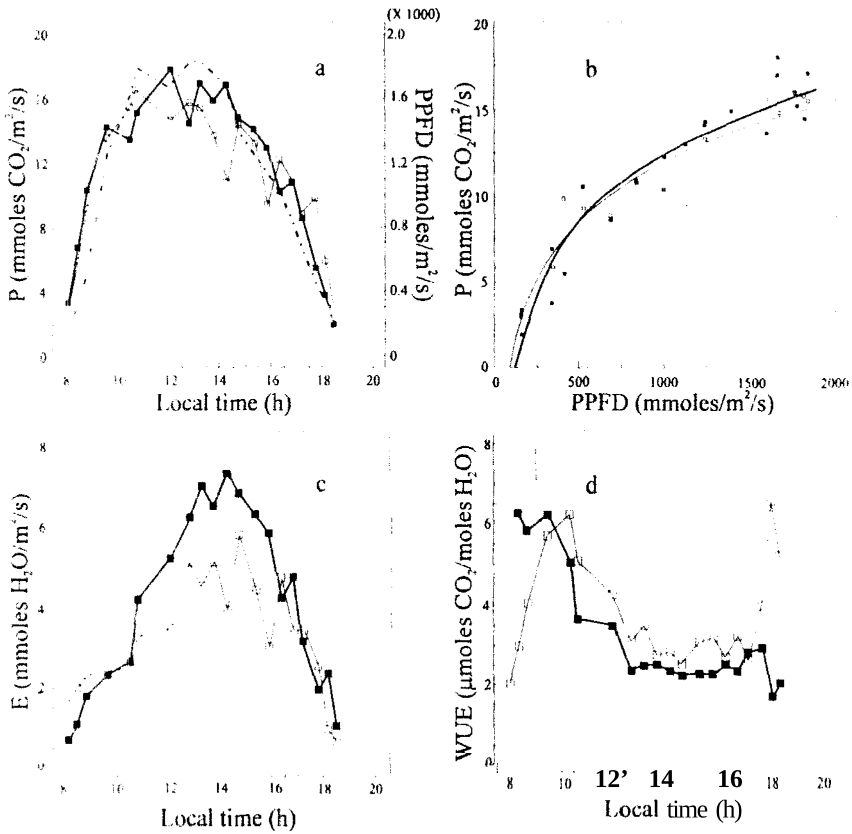
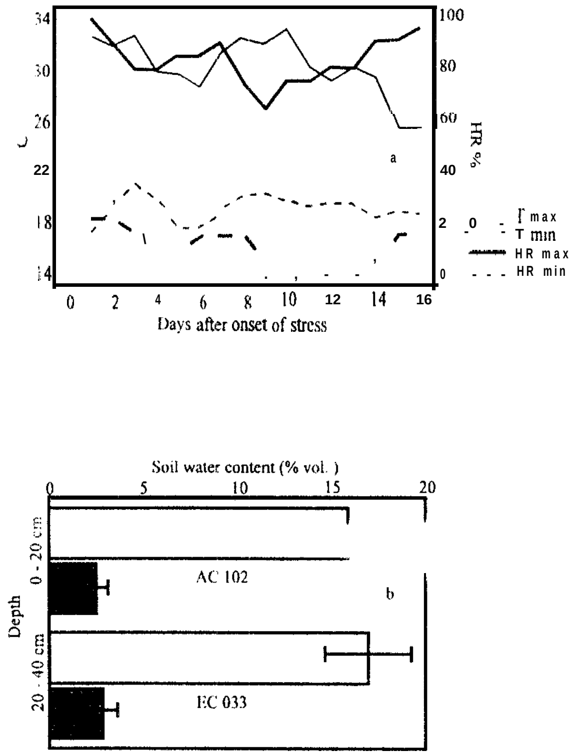


Fig. 2. Changes in (a) daily air temperature and relative humidity, and in (b) soil water content from the 1st (open bars) to the 15th day (shaded bars) of water stress Horizontal lines represent the mean interval of confidence P = 0.05.



Responses to water stress

Climatic and soil water conditions

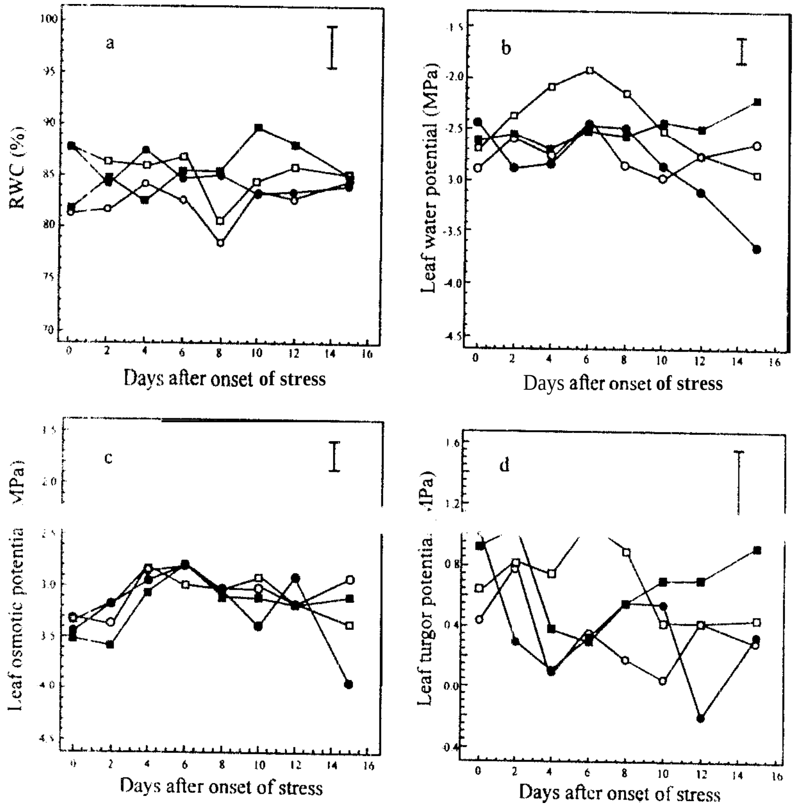
During the stress period the maximum air temperature (Tmax) and the minimum air temperature (Tmin) ranged between 27-34°C and 14-19°C respectively (fig. 2a) The maximum and minimum air humidity, RHmax and RHmin, were between 5.5959 % and 20-30% respectively.

Water relations

During the stress period, no significant differences in mid-day leaf RWC were observed between stressed and control plants. The mid-day leaf RWC in the stressed plants was between 77-87% in both genotypes, and between 82-90% in the controls (fig 3a). These results suggest that both EC033 and AC102 have an appreciable capacity to avoid the dehydration of their leaf tissues. Effects of water stress on ψf were observed only in AC102 after 12 days of treatment. The mean mid-day ψf on the 15th day of stress in the stressed plants (-3.7 MPa) was 1.5 MPa lower than those in the control plants (-2.2 MPa) (fig 3b) No significant differences in ψf were observed between stressed and control plants in EC033, and on the 15th day of treatment the mean ψf in all plants of EC033 was -[illegible] 7 MPa.

These results also suggested that EC033 has a higher capacity than AC 102 to avoid dehydration of its leaf tissues during water stress, The values of mid-day ψf observed in *Pachyrhizus* during the experiment were very low compared to those of earlier studies on other leguminous plants cultivated under the same conditions (Annerose, 1990. Nwalozie *et al.* 1992) No precise explanation for such low values could be drawn from this experiment However, it can bc hypothesized that the high evaporative demand observed during the experiment may have imposed an atmospheric water stress on the plants Nevertheless the development of such low ψf may contribute to maintenance of high leaf RWC through the establishment of a high water potential gradient between roots and leaves. The mid-day mean ψos measured within 12 days of stress were similarly very low, and they were not different between genotypes and treatments (fig. 3c). Differenccs in ψos were observed only in AC102 on thc 15th day when mean ψos in the stressed plants (-1.0 MPa) was 1 1 MPa lower than that in the control plants (-2.9 MPa) This osmotic adjustment in AC 102 contrihuted to the maintenance of ψt close to those observed in the control plants of EC033 (fig. 3d) Maintenance of leaf turgescence through osmotic adjustment constitute a powerful mechanism to tolerate leaf dehydration (Turner, 1986) The level of osmotic adjustment observed in AC1 02 indicates that this variety has a good drought tolerance.

Fig. 3 Changes in time of(a) relative water content, (b) leaf water, (c) osmotic, and (d) turgor potential in *Pachyrhizus*. Vertical lines represent the mean interval of confidence P = 0.05; (■, ●) AC102 controls and water-stressed respectively; (□, ○) EC033 controls and water-stressed respectively.



Stomatal conductance and gas exchange

From the fourth day of water stress to **the** termination of stress. the mid-day stomatal conductance (Gs), transpiration (E), and photosynthesis (P) were significantly reduced in the stressed plants of both varieties (fig. 4) subjected to the same treatment. By the 15th day ofwater stress the stomata were closed in the stressed plants of the 2 varieties, resulting in the extremely low values of E and P. The similar patterns of mid-day gas exchange responses in the stressed plants of EC033 and AC 102 do not reflect the differences observed in their water relations pattem (fig. 3) and values observed in the preliminary studies of plants grown under adequate soil moisture conditions (fig. 1). Whether these similar pattems between the 2 genotypes arc due solely to the water stress treatment or an additional effect of an atmospheric stress. i.e. high evaporative demand, needs to be further studied. Responses of stressed plants may therefore be monitored at the scale of the day.

Watcr stress effects on daily KWC, Gs, and gas exchange

Significant differences in daily responscs of EC033 and AC102 were observed at the scale of the day as illustrated on the 15th day of water stress (fig. 5). The responses in the stressed plants of the two species were thc same until mid-day hut EC033 maintained significally higher RWC, Gs, E, and P after mid-day. The RWC of AC102 was reduced from 87.5 to 77.0% between 08:00 and 17:00 h, while EC033 mamtained a stabilized RWC (83%) during all the day (fig. 5a). In stressed plants these values were associated with an important reduction of the gas exchange rates mcasured at 17:00 h in AC102, while EC033 cxhibited high values of P (4.5 μmoles $CO_2/m^2/sec^{-1}$) and E (1.5 mmoles H_2O/m^2 sec^{-1}) after 15 days ofwater stress. These results confirm the capacity of EC033 to ensure a better regulation of its leaf tissue water loss resulting in a better gas exchange activity and a maintenance and growth of leaf tissues.

Watcr stress effects on yield

Under well irrigated conditions EC033 exhibited a higher total yield (200 g/plant) than AC102 (KO g/plant) (fig.6). Tubers represented 94% of the total plant yield in EC033 and 59% in AC102. Water stress trcatmcnt resulted in a diminution of 10.6% and 47.4% of the total production in AC 102 and EC033, respectively. The tuber proportion of total plant yield incrcascd in stressed plants of AC1OI (+14%), whcreas it decreased in EC033 (- 14%). Flowers were not removed from thc plants during thc experiment. and competition between pods and tubers may have affected tuber yield observed in the two species (Noda *et al.*, 1983) Nevertheless, AC102 exhibited a better ability to maintain higher plant yields in terminal drought conditions than EC033.

Fig. 4. Changes with time of leaf (a) stomatal conductance, (b) transpiration, and (c) photosynthesis in *Pachyrhizus*. Vertical lines represent the mean interval of confidence P = 0.05; (■ , ●) AC102 controls and water-stressed respectively; (□ . ○) EC033 controls and water-stressed respectively.

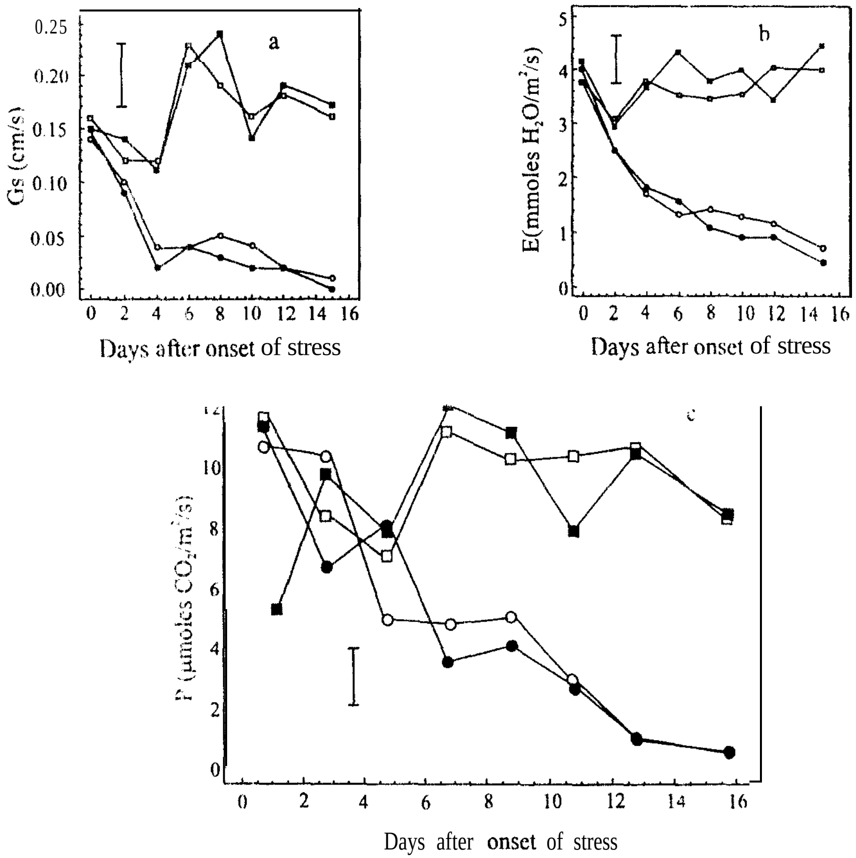


Fig. 5. Changes of leaf (a) relative water content. (b) stomatal conductance. (c) photosynthesis, and (d) transpiration in *Pachyrhizus* on the 15th day after beginning of water stress treatment. Vertical lines represent the mean interval of confidence P = 0.55; (■, ●) AC102 controls and water-stressed respectively; (Cl , 0) EC033 controls and water-stressed respectively.

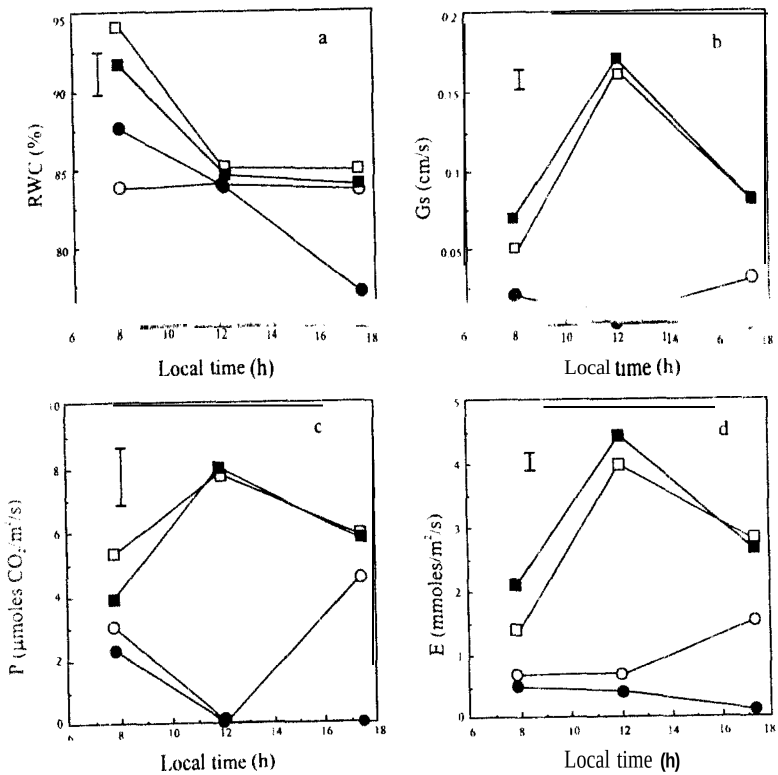
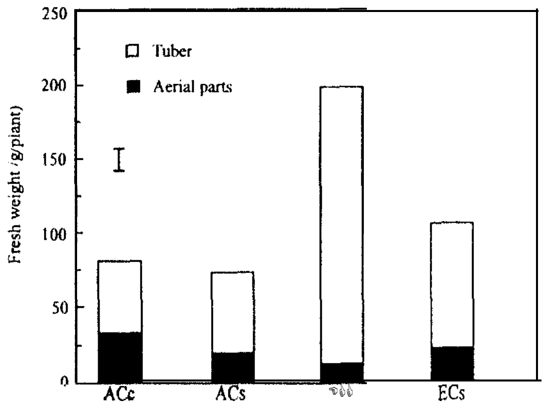


Fig. 6 Effect of 15 days of drought during the R7 stage on tuber and aerial parts of two genotypes of *Pachyrhizus*, EC033 (EC) and AC102 (AC); (ACc and ECc) control; (ACs and ECs) water-stressed. Vertical lines represent the mean interval of confidence P= 0.50



CONCLUSION

Although, the nimber of species surveyed in this study was small (2), the existence of some diversity within the genus has been demonstrated. EC033 exhibited a conservative strategy in regard to available water. This reaction has been characterised in this variety at the scale of the leaf by a reduction of water consumption through stomatal control, resulting in a better water use efficiency On the contrary, however, AC 102 exhibited an evasive strategy in quickly consuming available water, at the same time attaining high level of P, and this prohably enabled the plant to complete its cycle fast. A high capacity of osmotic adjustment in AC102 helped it to tolerate high levels of leaf dehydration. The determination of the hest drought adaptation strategy between those characterized in these two species is strictly dependent on the kind of drought they may experience. Depending on the intensity, the date of manifestation, and the duration of drought, each of them could be considered as an adaptive strategy. Under the conditions of water stress applied during objective. However, if more interest is to be given to yield stability, as in Sahelian areas, the suategy of AC 102 must be preferred.

Further studies are in progress at Bambey (Senegal) in order to describe the responses of *Pachyrhizus* to drought. At present, these studies are focused on the description of root development, carbon assimilation and its transfer within the plant, and quantification of water use at the crop level. As can be seen from the present paper, there is some diversity in physiological and agronomical responses of *Pachyrhizus* to drought. This diversity can be exploited to identify well adapted material and to increase yield under the prevalent dry conditions of Sahelian amas.

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