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Leaf gas exchange of *Pachyrhizus ahipa* and *P. erosus* under water and temperature stress

E.O. LEIDI

Dpto Biología Vegetal, IRNAS-CSIC, Avda Reina Mercedes 10, E-41012 Sevilla, Spain

Abstract

Gas exchange, water relations, and leaf traits were studied in the tuberous-root producing legumes ahipa (*Pachyrhizus ahipa*) and yambean (*P. erosus*) under different environmental conditions. Differences in leaf traits (hairiness, leaf area, areal leaf mass, stomatal density) and paraheliotropism were found between ahipa and yambean. Under sufficient water supply, the increase in air temperature and decrease in air humidity increased stomatal conductance (g_s) and net photosynthetic rate (P_N) in yambean but reduced them in ahipa. In a drying soil (14 d after irrigation), inter-specific variation in gas exchange was only observed in the early morning, and yambean showed a greater sensitivity to water restriction than ahipa. High g_s at low humidity increased P_N of *P. erosus* but resulted in lower water-use efficiency (WUE). However, long-term WUE, estimated by leaf carbon isotope discrimination, showed little variation between species. Daily-irrigated ahipa and yambean grown in the greenhouse did not show significant differences in gas exchange. However, leaf temperature was significantly greater in yambean than in ahipa while a steepper relationship between E and P_N and g_s was observed in ahipa.

Additional key words: ahipa; carbon isotope discrimination; photosynthesis; stomatal conductance; transpiration; water-use efficiency; yambean.

Introduction

Ahipa [*Pachyrhizus ahipa* (Wedd.) Parodi] is a tuber-producing legume cultivated at high altitude in the Andean region of Bolivia and Northern Argentina (Ørting *et al.* 1996). Its tropical relative, the Mexican yambean [*P. erosus* (L.) Urban] is commercially grown in areas of Mexico, Thailand, China, and Malaysia (Sørensen *et al.* 1997).

There is scarce information on the eco-physiology of the species and studies of adaptation of *Pachyrhizus* species have been mainly focussed on root yield in several tropical or subtropical environments (Arévalo 1998, Espinoza *et al.* 1998). Results of preliminary studies with *Pachyrhizus* spp. under drought stress have shown differences in gas exchange parameters among species (Annerose and Diouf 1994, Adjahossou and Adé 1998). In ahipa landraces, photosynthetic electron transport and photosystem 2 activity were differentially affected by drought stress (Matos *et al.* 1999) which might be related to the variation in membrane stability under drought and high temperature stress (Campos *et al.* 2000).

Root starch and sugar are the main products of ahipa (Leidi *et al.* 2002) and maintenance of high photosynthetic rates during the growth season would promote root yield and starch and sugar contents in the roots. Changes in stomatal conductance (g_s) by water stress (drying soils, high air temperature, and low relative humidity), and its effect on gas exchange (photosynthesis, transpiration) and leaf temperature, affect water-use efficiency (WUE) and productivity of crops (Lawlor 1995). The growth season for ahipa in the Mediterranean area is characterised by high evapotranspiration rate, with high air temperature and high air vapour pressure deficits. Furthermore, drought is a frequent constraint in the region and there is a need for highly efficient water-using crops. To determine the adaptation capacity of *Pachyrhizus* species to Mediterranean conditions and identify selection traits for breeding, the aim of the present work was to study leaf gas exchange and leaf water relations in ahipa and yambean over a range of air temperatures and soil water contents.

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Fax: +34 954624002; e-mail: leidi@irnase.csic.es

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Materials and methods

Field experiments: Field trials were located at Las Torres (Alcalá del Río, typic xerofluvent soil) and La Hampa (Coria del Río, typic xerochrept soil), both sites located in the province of Seville (SW Spain). At Las Torres, the study was restricted to ahipa [*Pachyrhizus ahipa* (Wedd.) Parodi] accessions AC102 and AC229. At La Hampa, three different species were planted: ahipa AC521, Mexican yambean [*P. erosus* (L.) Urban EC201], and Amazonian yambean [*P. tuberosus* (Lam.) Spreng. TC353]. The sowing date was 25th April 2000. No fertilisation or insecticides were applied. Furrow irrigation to reach soil field capacity was performed every two weeks. No rainfalls were recorded during the period of study. The experimental design was a completely randomised block design with six replications. The plots were 6 m long, with rows spaced 0.5 m apart.

Pot experiments: In the summer 2001, ahipa (AC521) and yambean (EC201) plants were grown in greenhouse using 20 000 cm^3 plastic pots filled with 15 kg of potting mix. Gas exchange and temperature measurements were then carried out on flowering plants that did not suffer water constraints during the growth cycle.

Physiological parameters were determined in field-grown plants before and after irrigation at two times during the day to get conditions of different soil water availability and air vapour pressure deficit (VPD). Measurements were initiated at flowering and performed several times during the growing season. Measurements of single-leaf net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were made with an open system using a portable infrared gas analyser (*LCA-2*, *Analytical Development Co.*, Hoddesdon, England) equipped with a Parkinson leaf chamber and a data logger. The measurements were made at 10:00 and 13:00 at saturating photosynthetic photon flux densities (*ca.* 1 500 $\mu\text{mol m}^{-2}\text{ s}^{-1}$) on the youngest fully expanded leaves (five replications). An estimate of instantaneous water-use efficiency (P_N/g_s) was calculated for reducing the effects of ambient vapour pressure between measurements on transpiration (Leidi *et al.* 1999). Determination of sub-stomatal CO_2 concentration was made according to Caemmerer and Farquhar (1981). For the determination of leaf water potential (ψ_l) and leaf water content (LWC), leaves were harvested immediately after gas exchange measurement, kept in plastic bags in an ice-box, water potential was determined in a Scholander bomb, and then they were weighed and dried (48 h, 70 °C). Before drying, leaf area was measured using *Delta-T* image analysis system (*DIAS*, *Delta-T Devices*, Cambridge, U.K.) and the areal leaf mass (ALM) was calculated.

Dried leaves from different replicates were combined and ground to fine powder. C isotope composition was then analysed by mass spectrometry in the laboratory of Prof. G. Farquhar (Environmental Biology Group, RSBS, Australian National University, Canberra, Australia).

Leaf epidermis sampling from adaxial and abaxial surfaces were prepared with cyanoacrylate adhesives (Wilson *et al.* 1981) for morphological studies using an optical microscope.

Leaf temperature (T) was measured with a hand-held infrared thermometer (model *RAY R2 PAG*, *Raytec*, Santa Cruz, California, USA) targeting single, upper canopy fully sunlit leaves at midday. Air temperature and humidity at canopy level were measured simultaneously with an electronic device (*HOBO* data logger, *Onset Comp.*, Pocasset, Massachusetts, USA). The variable ΔT was calculated as the difference between air temperature and leaf temperature.

Leaf N content was determined after Kjeldahl digestion of dried samples and ammonium measured by a colorimetric reaction (phenol-hypochlorite) in an *Auto-Analyzer* (*Bran+Luebbe*, Norderstedt, Germany). Leaf K content was determined by atomic absorption spectrophotometry.

All parameters were statistically analysed using analysis of variance. Statistical differences among genotypes for traits were tested with Fischer's least significant difference test ($p<0.05$). Relationships between traits were determined using Pearson's simple correlation test.

Results

Leaf traits: Yambean showed greater leaf area than ahipa at both field and greenhouse conditions (Table 1). However, ahipa leaves from field-grown plants showed greater areal leaf mass than yambean (Table 1). Leaf epidermis of ahipa and yambean differed in the amount and size of trichomes (Fig. 1), with ahipa presenting more long trichomes per unit leaf area. Number and distribution of stomata between adaxial and abaxial leaf surfaces also differed between species (Fig. 1). Yambean showed stomata on both adaxial and abaxial surfaces and higher number of stomata per unit leaf area than ahipa on the abaxial surface. In the field, paraheliotropism was observed in ahipa leaves with rising temperatures, while yambean leaves remained largely unaffected, fully exposing the leaflets to the sun. In greenhouse grown plants, both ahipa and yambean showed paraheliotropic movement when exposed to high temperature.

Gas exchange in the field: In field-grown plants, increase in VPD during the day led to significant increases in g_s of yambean (Table 2), whereas no significant variation, or even a trend to decrease, was found in ahipa. The differential responsiveness of stomata between both species affected P_N and E (Table 2). In general, yambean showed higher P_N than ahipa at high temperatures and VPD except at 14 d after irrigation. At that time, with less soil water available to plants, significant differences in leaf water content and water potential between species were recorded. However, no significant differences in gas exchange were found and both species presented water-stress related inhibition of g_s and P_N. No significant differences in carbon isotope discrimination between ahipa and yambean were found (Table 3).

Table 1. Areal leaf mass (ALM) and area of individual leaves used for gas exchange from plants of ahipa (*P ahipa*) and yambean (*P. erosus*) grown in the field or the greenhouse. Means in columns followed by the same letter are not significantly different (LSD test, $p<0.05$).

	Field		Greenhouse	
	ALM $[\mathrm{g\,m^{-2}}]$	Leaf area $[\mathrm{cm^2}]$	ALM $[\mathrm{g\,m^{-2}}]$	Leaf area $[\mathrm{cm^2}]$
ahipa	64 a	120 a	17 a	460 a
yambean	48 b	330 b	25 b	570 b

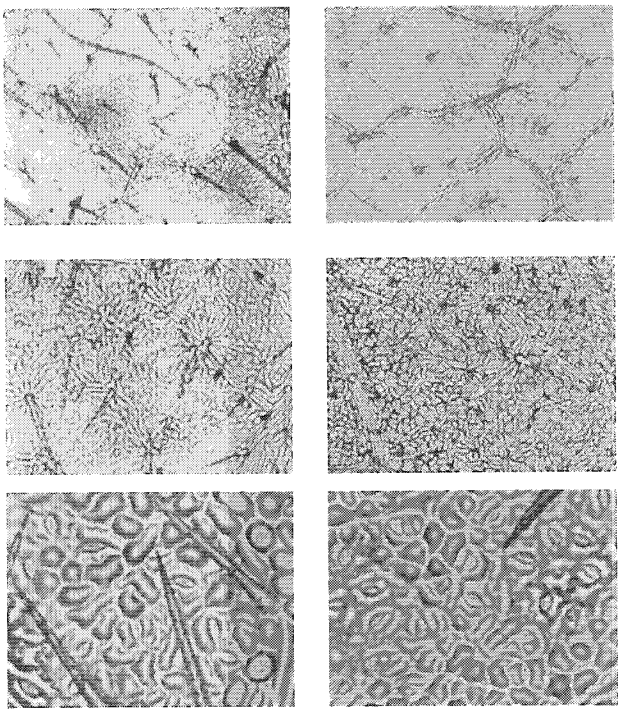

Fig. 1. Adaxial (upper) epidermis (*P. ahipa, top left*; *P. erosus, top right*) and abaxial (lower) epidermis (*P. ahipa, centre and bottom left*; *P. erosus, centre and bottom right*).

Differences in WUE between ahipa and yambean were detected only when soil water availability was high (at 90 and 110 DAS, Table 2), with ahipa showing higher WUE than yambean at high VPD.

At high temperature and VPD, leaf water content was greater in yambean than in ahipa (Table 2), while differences in leaf water potential between both species were only recorded when soil water availability diminished after 14 d from last irrigation (Table 2).

Ahipa and yambean leaves also differed in the leaf content of N and K (Table 4). Consistently, ahipa contained more N but less K than yambean except when leaf samples were obtained under water limitation (Table 4). A significant association was found among leaf K content and g_s ($r = 0.76$, $p<0.001$), P_N ($r = 0.61$, $p<0.01$), E ($r = 0.59$, $p<0.01$), leaf water content ($r = 0.63$, $p<0.01$), and leaf water potential ($r = 0.47$, $p<0.05$)

Gas exchange in the greenhouse: Daily irrigated potted ahipa and yambean plants exposed to different ranges of air temperatures showed no significant differences in P_N and E (values not shown) but significant differences in g_s at the highest air temperatures (Fig. 2). Only in yambean leaves g_s increased at the highest temperature. When plotting E and P_N against g_s, different slopes were observed which might indicate differential sensitivity of both physiological processes to stomata closure (Fig. 3).

Shaded and sunlit leaves of ahipa and yambean showed differences in leaf temperature (Fig. 4) with yambean generally presenting greater leaf temperature.

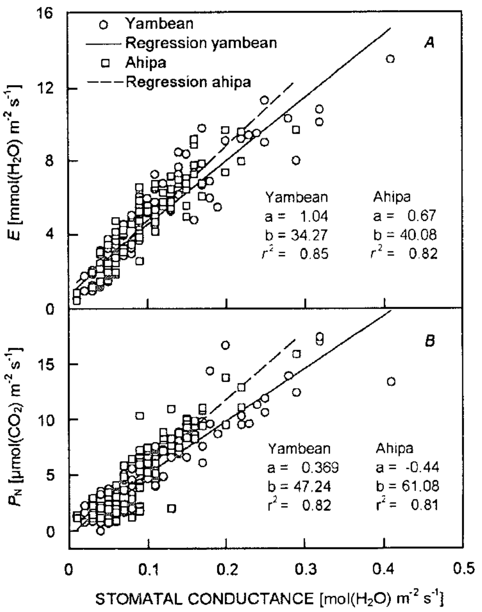

Fig. 2. Relationship between stomatal conductance, g_s and transpiration rate, E (*A*) or net photosynthetic rate, P_N (*B*) in *Pachyrhizus erosus* EC201 and *P. ahipa* AC521 plants grown in pots.

Table 2. Net photosynthetic rate, P_N [μmol(CO$_2$) m^{-2} s^{-1}], stomatal conductance, g_s [mol(H$_2$O) m^{-2} s^{-1}], transpiration rate, E [mmol(H$_2$O) m^{-2} s^{-1}], water use efficiency, WUE [μmol mol^{-1}]), leaf water content, LWC [kg kg^{-1}(dry mass)], and water potential, ψ_l [MPa] in ahipa and yambean at different air temperature and VPD at 3 d after irrigation (90 d after sowing, DAS), 14 d after irrigation (104 DAS), and 3 d after re-watering (110 DAS). For each environmental condition, means in columns followed by the same letter are not significantly different (LSD test, $p<0.05$).

		P_N	g_s	E	WUE	LWC	ψ_l
90 DAS, 22.3 °C, –1.13 kPa	ahipa	17.0 a	0.40 a	9.0 a	44.3 a	2.8	8.5
	yambean	17.5 a	0.47 a	10.7 b	37.9 a	nd	nd
90 DAS, 27.5 °C, –2.37 kPa	ahipa	15.4 a	0.33 a	9.5 a	48.4 a	2.5 a	9.8 a
	yambean	20.6 b	0.66 b	12.7 b	32.2 b	3.3 b	7.8 a
104 DAS, 29.0 °C, –3.2 kPa	ahipa	8.8 a	0.16 a	4.5 a	61.2 a	3.2 a	7.5 a
	yambean	5.6 a	0.08 b	3.4 a	74.0 b	3.6 b	5.8 a
104 DAS, 35.3 °C, –4.18 kPa	ahipa	5.2 a	0.16 a	8.3 a	32.0 a	3.0 a	8.1 a
	yambean	7.4 a	0.20 a	9.4 a	35.9 a	3.3 a	10.9 b
110 DAS, 26.5 °C, –2.01 kPa	ahipa	15.8 a	0.41 a	8.4 a	38.9 a	2.9 a	6.8 a
	yambean	10.1 b	0.22 b	6.4 b	48.3 b	3.2 b	6.1 a
110 DAS, 31.2 °C, –3.30 kPa	ahipa	13.9 a	0.37 a	11.2 a	38.2 a	2.6 a	8.7 a
	yambean	15.0 a	0.49 b	12.8 b	31.2 b	3.1 b	9.6 a

Table 3. Variation in carbon isotope discrimination (Δ) by leaves of ahipa accessions (AC102, AC229, AC521) and yam bean plants (EC201, TC353) grown at Las Torres and La Hampa sampled on different days after sowing (DAS) with different levels of soil water availability.

Las Torres	Δ [‰] 65 DAS	 98 DAS	 111 DAS	La Hampa	Δ [‰] 90 DAS	 104 DAS	 110 DAS
AC102	19.21	19.84	19.42	AC102	18.90	18.90	18.79
AC229	19.32	19.84	19.42	AC521	18.27	19.11	19.00
				EC201	19.21	18.79	18.38
				TC353	18.90	19.00	18.48

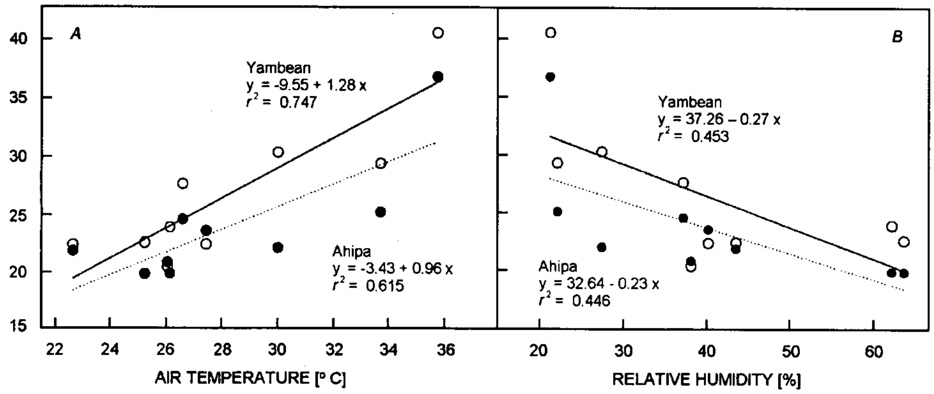

Fig. 3. Relationship between air temperature (*A*) or relative humidity (*B*) with leaf infrared temperature from ahipa and yambean plants grown in pots. Plotted values are from different records taken on consecutive days at different times of the day.

Comparison of ahipa accessions: When soil water reserves were gradually diminished 7 d after irrigation, significant differences in E between the landraces AC102 and AC229 were observed (Table 5). Increase in air temperature led to stomatal closure and inhibition of P_N (see 65 DAS, Table 5) as it was found in the interspecific comparisons (Table 2). Differences in WUE (based on gas exchange values) between AC102 and AC229 were also recorded, with AC102 showing normally higher WUE than AC229 except when no soil water limitation could be expected (1 d after irrigation) (Table 5).

Leaf water and osmotic potentials showed significant variation between landraces only at 98 DAS (Table 5). The landrace AC229 was able to maintain lower leaf temperatures than AC102 only in some sampling dates.

The differences in g_s and E, affecting WUE, were not reflected in carbon isotope discrimination (Table 3), which showed little variation between landraces.

Discussion

In plants grown in the field, increase in air temperature and VPD at midday led to an increase in g_s in yambean but a decrease in ahipa. Yambean showed greater leaf water content than ahipa, but no significant differences in leaf water potential between species were observed. Leaf area, area leaf mass, and number and distribution of stomata also showed inter-specific variation (Table 1, Fig. 1). In greenhouse-grown plants, significant differences between species were only detected in g_s at the largest range of temperature (Fig. 2). Differences were also found in the slope of the regression g_s *versus* P_N and E (Fig. 3) and in leaf temperature (Fig. 4).

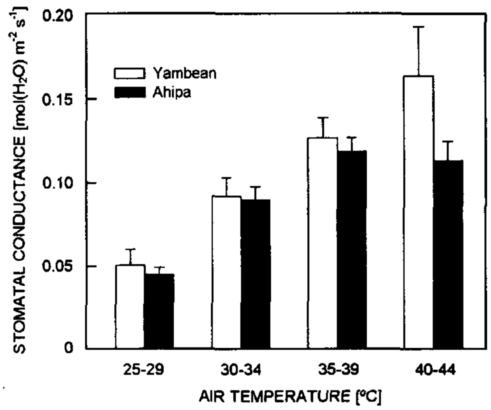

Fig. 4. Stomatal conductance at different sets of air temperature ranges in yambean and ahipa plants grown in pots without water limitation. *Vertical bars* represent the standard error of the mean.

Table 4. Nitrogen and potassium contents in leaves of ahipa and yambean sampled at different days after sowing (DAS) during the growth cycle [g kg^{-1}(dry mass)]. Means in columns followed by the same letter are not significantly different (LSD test, $p<0.05$).

	90 DAS		104 DAS		110 DAS	
	N	K	N	K	N	K
ahipa	37 a	12 a	33 a	14 a	33 a	13 a
yambean	28 b	39 b	32 a	17 a	29 b	17 b

Considering the inter-specific differences in paraheliotropic movement, distribution and density of stomata and trichomes, ALM, leaf area, and N content, the variation observed, probably resulting from evolution under contrasting environments, provided the species with different strategies for adaptation to extreme conditions. With smaller and thicker hypostomatous leaves, and probably more densely packed mesophyll cells, ahipa showed an adaptative strategy for maintaining P_N under stress (drought, temperature) similar to other plant species (Fischer and Turner 1978, Smith *et al.* 1997).

In ahipa, the stomatal closure in response to an increase in the ambient VPD might be caused by a deficit of water supply from the xylem to the guard cells (Nonami *et al.* 1990). This phenomenon may serve as a water saving mechanism by reducing transpiration water loss at high VPD, while the consequent temperature built-up is resolved with changes in leaf orientation (paraheliotropism, see below). At high VPD and without water limitations, yambean leaves showed high g_s (Table 2) and no need for paraheliotropic movements because of efficient evaporative cooling.

The environmental differences among greenhouse and field conditions might have modified stomatal response as it did in leaf traits like leaf area and ALM (Table 1). In well irrigated pot-grown ahipa plants, the limitation of g_s at the highest temperatures (Fig. 2) and the steeper relationship of g_s with both E and P_N (Fig. 3) might represent a more sensitive stomatal reaction to the increase in temperature and VPD.

Yambean leaves had higher water and K contents than ahipa leaves over a range of environmental conditions in the field (Tables 2 and 4). The significant association found between K accumulation and gas exchange and leaf water content and water potential may be based upon the direct involvement of K in stomatal movement (Hinckley and Braatne 1994) and osmoregulation (Hsiao and Läuchli 1986). The higher leaf K content in field-grown yambean plants (Table 4) may have improved its osmotic adjustment and water uptake (Table 2), thereby increasing g_s (and E) at high VPD. Several reports have related K supply and plant water relations (Lindhauer 1985) and growth improvement under drought (Premachandra *et al.* 1993, Sangakkara *et al.* 2001).

Leaf paraheliotropic movements (change in laminae orientation parallel to the sun's direct beam) contribute to reduce leaf temperature and leaf to air VPD gradient (Prichard and Forseth 1988). At high temperature and high evaporative demand, leaf paraheliotropism may reduce transpiration water loss and improve WUE (Ehleringer and Forseth 1989). This mechanism might be particularly important if the plant is experiencing soil water limitation in order to avoid temperature built-up and damage to photosynthetic machinery (Rosa *et al.* 1991). The differential display of paraheliotropism between species was evident in the field, where ahipa quickly folded leaflets in response to the increase in VPD.

When grown in the field, ahipa adapted better than yambean to water stress by showing reduced leaf area and increasing ALM (Table 1) while presenting additional traits like leaf trichomes and stomatal distribution which may improve water economy under limiting conditions (Fischer and Turner 1978, Smith *et al.* 1997).

Although stomata closure determines a short-term penalty to photosynthetic carbon gain by the stomatal limitation to CO_2 diffusion, it reflects a conservative strategy that may improve the plant performance in the long-term by reducing soil water use (Quizenberry 1982). In fact, yambean showed a higher sensitivity to water loss (lower leaf water potentials than ahipa) at low water availability (104 DAS, Table 2) and lower recovery of gas exchange after re-supplying water (110 DAS, Table 2).

In conclusion, differences in leaf area and morphology (hairiness, stomatal density, ALM) jointly with differences in gas exchange and water content between ahipa and yambean might be the result of evolutionary adaptations to their natural environments. The combination of traits found in ahipa affecting heat balance (paraheliotropism, hairiness, leaf size) and water economy (g_s) may improve its physiological performance in drought-prone environments. In the context of typical dry Mediterranean summer, where high temperature and low air humidity frequently combine with restricted availability of irrigation water, ahipa seems better adapted for crop production with an efficient use of limited resources.

Table 5. Net photosynthetic rate, P_N [μmol (CO_2) m^{-2} s^{-1}], stomatal conductance, g_s [mol(H_2O) m^{-2} s^{-1}], transpiration rate, E [mmol(H_2O) m^{-2} s^{-1}], water use efficiency, WUE [μmol mol^{-1}], leaf water content, LWC [kg kg^{-1}(dry mass)], leaf water potential, ψ_l, and osmotic potential, ψ_o [MPa], and leaf temperature, ΔT [°C] in two *Pachyrhizus ahipa* accessions. Measurements were taken at different times during the day (65 DAS) and days after irrigation during the growing season for sampling under different environmental conditions. For each environmental condition, means in columns followed by the same letter are not significantly different (LSD test, $p<0.05$).

		P_N	g_s	E	WUE	LWC	ψ_l	ψ_o	ΔT
65 DAS, morning (7 d, 32 °C)	AC102	15.0 a	0.51 a	9.5 a	30.6 a	3.2 a	7.4 a	7.2 a	1.9 a
	AC229	18.5 a	0.71 a	12.4 b	26.6 a	3.2 a	7.6 a	5.8 a	3.2 b
65 DAS, midday (7 d, 37.5 °C)	AC102	13.6 a	0.38 a	10.2 a	37.4 a	3.1 a	7.9 a	8.2 a	2.0 a
	AC229	16.9 a	0.64 b	15.7 b	26.8 b	3.2 a	8.2 a	8.8 a	4.7 b
81 DAS (1 d, 29.5 °C)	AC102	20.8 a	0.89 a	14.2 a	23.9 a	3.2 a	nd	nd	7.6 a
	AC229	22.4 a	0.71 a	11.5 a	35.1 b	2.8 b	nd	nd	8.4 a
98 DAS (7 d, 33.0 °C)	AC102	19.7 a	0.82 a	13.1 a	25.0 a	3.1 a	7.6 a	7.6 a	7.8 a
	AC229	22.6 b	1.11 b	15.6 b	21.3 b	2.7 b	9.4 b	8.6 b	13.4 b
111 DAS (9 d, 34.9 °C)	AC102	21.4 a	0.90 a	13.5 a	24.6 a	2.9 a	8.4 a	7.6 a	3.4 a
	AC229	21.5 a	0.87 a	14.3 a	25.3 a	2.9 a	6.0 b	7.8 a	3.6 a

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