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Gas exchange in umbu tree accessions

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Abstract

The objective of this work was to evaluate gas exchanges in umbu tree accessions. A 5 × 7 × 2 split-split plot experiment was carried out in a completely randomized design (five accessions – BRS-68, EPAMIG-05, BGU-61, BGU-75, and BGU-50 × seven evaluation dates × two reading times – 8 a.m. and 2 p.m.) with three repetitions. The lower leaf temperatures recorded in BRS-68 and EPAMIG 05 accessions favor higher net photosynthetic rates, water use efficiency and instantaneous carboxylation efficiency compared to BGU 61 accession. Umbu tree regulates transpiration by reducing stomatal conductance under high vapor pressure deficit, although the tree increases transpiration as a defense strategy against heat stress, even with a reduction in stomatal conductance. High temperatures limit instantaneous carboxylation efficiency, photosynthetic rate, and the ratio of photosynthesis to radiation incident on the leaf. Transpiration varies directly with stomatal conductance, while intrinsic water use efficiency varies inversely with internal CO_2 concentration.

Keywords: correlation, ecophysiology, genotypes, *Spondias tuberosa*

Introduction

The umbu tree (*Spondias tuberosa*) is a xerophytic, deciduous fruit tree, belonging to the Anacardiaceae family (Mertens et al., 2016). Although native and endemic to the Caatinga biome, the tree is also affected by stresses caused by climatic conditions of the Brazilian semi-arid region, which can reduce severely fruit production (Menezes et al., 2017). However, characteristic morphophysiological adaptations of the species, such as xylopodia – underground, woody organs for water and nutrient storage – allow osmotic adjustment, high stomatal resistance, leaf senescence and abscission during the dry season. Such adaptations reduce transpiration and increase water use efficiency, thereby avoiding water deficit (Lima et al., 2018; Dias et al., 2019; Silva et al., 2019; Pedrosa et al., 2020) and allowing umbu tree cultivation under rainfed conditions.

The adaptation of umbu trees to stressful levels of temperature, light intensity and water scarcity needs to be evaluated to avoid, when under extreme events, the reduction of yield capacity. Genotypic adaptations can be identified by the maintenance or not of physiological activities, for example, photosynthesis and transpiration, when different accessions are subjected to the same stressful environmental condition. Such adaptations can be assessed from the observation of physiological responses to environmental conditions, which may shed light on plant needs and possible improvements in crop management (Silva et al., 2019; Santos et al., 2021).

Assessing gas exchanges allows characterizing genotypes through physiological responses to local conditions (Donato et al., 2022), establishing genotypic variation and guiding the choice of accessions that are more adapted to site-specific conditions. The effect of the interaction between gas exchange and environmental variations can instantly correlate with productivity

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(Arantes et al., 2016; Santos et al., 2021).

Thus, the objective of this work was to evaluate gas exchange in umbu tree accessions.

Material and Methods

The study was carried out in the collection of umbu accessions at the Instituto Federal Baiano, campus Guanambi, Bahia, Brazil (14°17'32''S, 42°41'34''W, and altitude of 547 m), in Red-Yellow Latosol (Oxysol). The climate is semi-arid, hot and dry, with a well-defined dry season in winter and a rainy season between October and March. The average annual precipitation is 665 mm and the average annual temperature is 26 °C. Meteorological data recorded during the days and times of reading are shown in (**Table 1**).

The collection of accessions was implanted in 2007, in a quincunx spaced at 8 x 8 x 8 m. Crop management practices included topdressing fertilization at the beginning and at the end of the rainy season; phytosanitary control; weeding in the middle of the rainy season, after the end of the season and at the beginning of the dry season; and occasional pruning to remove shoots from the rootstock. The practices are in accordance with the recommendations in the literature (Lima et al., 2018; Donato et al., 2019a; Souza et al., 2020).

The experiment was carried out in a completely randomized design with treatments arranged in split-split plots, subdivided in time, with three replications. Five umbu accessions from different geographic origins were assigned to plots: BRS-68 (EPAMIG-01, Lontra, MG), EPAMIG-05 (Porteirinha, MG), BGU-61 (Januária, MG), BGU-75 (Macaúbas, BA), and BGU-50 (Santana, BA); seven evaluation dates to subplots: 12/02/2020, 12/23/2020, 01/19/2021, 02/12/2021, 04/14/2021, 04/27/2021, and 05/27/2021; and two reading times to sub-subplots: 8 a.m. and 2 p.m.

Gas exchange rates were measured from the rainy season to the beginning of the dry season (December to May) on leaves in the middle third of the canopy, between the 3rd and 5th fully expanded leaf pair, using an infrared gas analyzer (IRGA) model Lcpro+ ®Portable Photosynthesis System (ADC BioScientific Limited, UK), under ambient temperature and irradiance, air flow of 200 ml min^{-1} and, radiation shield facing the sun (Donato et al., 2022). The readings were incident leaf radiation - Q_{leaf} (μmol photons m^{-2} s^{-1}), leaf temperature - T_{leaf} (°C), internal CO_2 concentration - C_i (μmol CO_2 mol^{-1}), stomatal conductance - g_s (mol H_2O m^{-2} s^{-1}), transpiration - E (mmol H_2O m^{-2} s^{-1}), net photosynthesis – A (μmol CO_2 m^{-2} s^{-1}); instantaneous water use efficiency - WUE (μmol CO_2 m^{-2} s^{-1}/mmol H_2O m^{-2} s^{-1}), instantaneous carboxylation efficiency - A/C_i (μmol CO_2 m^{-2} s^{-1}/μmol CO_2 mol^{-1}), ratio of photosynthesis to incident radiation on leaves - A/Q_{leaf} (μmol CO_2 m^{-2} s^{-1}/ μmol photons m^{-2} s^{-1}), and intrinsic water use efficiency - A/g_s (μmol CO_2 m^{-2} s^{-1}/mol H_2O m^{-2} s^{-1}).

The data had no normal distribution when tested by the Lilliefors test; therefore, non-parametric Wilcoxon tests (for paired samples) and Kruskal Wallis tests (for independent samples) were used at 5% significance. Pearson's correlations were also estimated between the 10 physiological variables measured considering all accessions and per accession using SAEG statistical software – UFV®, version 9.1.

Table 1. Maximum (T_{max}) and minimum (T_{min}) temperature, mean relative humidity (RH), precipitation (P), reference evapotranspiration (ETo), vapor pressure deficit (VPD), Global Solar Radiation (Rad.T), mean wind speed ($Wind_{mean}$) and gust speed ($Gust_{Maximum}$) recorded on the days and times of the physiological measurements carried out in five accessions of umbu trees - Guanambi, BA

Date MM/DD/YYYY	Time	T_{max} (°C)	T_{min} (°C)	RH (%)	P (mm h^{-1})	ETo (mm h^{-1})	VPD (kPa)	Rad.T (MJ m^{-2} dia^{-1})	$Wind_{mean}$ (m s^{-1})	$Gust_{maximum}$ (m s^{-1})
12/02/2020	8 a.m.	25.70	24.10	72.00	0.00	0.36	0.72	42.60	3.10	6.30
12/02/2020	2 p.m.	32.70	32.10	42.00	0.00	0.69	2.20	82.08	0.90	4.00
12/23/2020	8 a.m.	25.40	23.70	78.00	0.00	0.23	0.56	31.54	0.90	4.00
12/23/2020	2 p.m.	32.20	31.40	47.00	0.00	0.46	1.95	48.90	0.90	4.00
01/19/2021	8 a.m.	24.90	23.60	62.00	0.00	0.36	0.95	36.12	4.90	12.10
01/19/2021	2 p.m.	32.70	31.20	41.00	0.00	0.74	2.19	84.07	2.70	7.20
02/12/2021	8 a.m.	24.40	22.80	68.00	0.00	0.30	0.77	31.36	4.90	11.20
02/12/2021	2 p.m.	30.30	29.60	54.00	0.00	0.74	1.54	83.72	3.10	7.20
04/14/2021	8 a.m.	27.00	25.50	45.00	0.00	0.46	1.52	41.39	5.40	10.70
04/14/2021	2 p.m.	33.70	32.60	32.00	0.00	0.61	2.68	66.87	1.80	5.80
04/27/2021	8 a.m.	26.70	25.00	70.00	0.00	0.25	0.81	29.20	1.80	0.00
04/27/2021	2 p.m.	31.40	31.20	44.00	0.00	0.38	2.01	38.53	1.30	4.00
05/27/2021	8 a.m.	24.90	23.20	67.00	0.00	0.30	0.81	39.31	1.80	4.50
05/27/2021	2 p.m.	32.40	31.90	41.00	0.00	0.46	2.21	47.17	2.20	6.70

Source: Meteorological data recorded at the automatic station at the Instituto Federal Baiano campus Guanambi, installed near the experimental area.

Results and Discussion

The physiological variables measured in the umbu tree accessions did not show a normal distribution, therefore, they were tested by non-parametric analyses (**Tables 2**, **3** and **4**).

Leaf temperature (T_{leaf}), internal CO_2 concentration (C_i), net photosynthesis (A), instantaneous water use efficiency (WUE), ratio of photosynthesis to incident radiation on the leaf (A/Q_{Leaf}), instantaneous carboxylation efficiency (A/C_i) and intrinsic water use efficiency (A/g_s) varied between accessions by the Kruskal-Wallis test, at 5% significance (Table 2). Incident radiation on the leaf (Q_{Leaf}), T_{Leaf}, C_i, transpiration (E), stomatal conductance (g_s), A, A/g_s, A/E, A/C_i and A/Q_{Leaf} varied between the evaluation dates (Table 3). For these variables, except for Q_{lleaf}, there was a difference between reading times based on the Wilcoxon test at 5% significance (Table 4).

A lower T_{leaf} was recorded for BRS-68 accession when compared to the others, except for EPAMIG 05. Photosynthetic rates, A/C_i and WUE were higher for BRS 68 and EPAMIG 05, compared to BGU 61, while BRS 68 and EPAMIG 05 were higher. BRS 68 showed higher A/Q_{leaf} compared to EPAMIG 05 (Table 2). Lima Filho and Aidar (2016) describe, from other works, a higher rate of net photosynthesis in BRS-68 accession and argue that this may be a characteristic associated with accessions bearing "giant" fruits, which can be a competitive

Table 2. Physiological characteristics recorded in five umbu tree accessions - Guanambi, BA

Accessions	T_{leaf}		C_i		A		WUE		A/Q_{leaf}		A/C_i		A/g_s	
BRS-68	38.00	B	285.19	AB	7.67	A	2.10	A	0.0066	A	0.0275	A	48.10	A
EPAMIG-05	39.10	AB	297.46	B	6.65	A	1.57	A	0.0051	B	0.0242	A	39.87	A
BGU-61	40.40	A	364.04	A	5.57	B	0.54	B	0.0058	AB	0.0191	B	11.77	A
BGU-75	40.40	A	332.87	AB	5.99	AB	0.89	AB	0.0058	AB	0.0205	AB	21.66	B
BGU-50	40.30	A	319.37	AB	5.88	AB	1.02	AB	0.0056	AB	0.0214	AB	24.26	B
Mean	39.70		319.84		6.35		1.23		0.0058		0.0225		29.10	
CV (%)	11.30		28.82		100.80		123.12		123.67		95.24		117.61	

Means followed by samel letters do not differ by the Kruskal-Wallis test at 5% significance. T_{leaf} – leaf temperature (°C); C_i – internal CO_2 concentration (μmol CO_2 mol^{-1}); A – net photosynthesis (μmol CO_2 m^{-2} s^{-1}); A/E – instantaneous water use efficiency ((μmol CO_2 m^{-2} s^{-1})(mmol H_2O m^{-2} s^{-1})$^{-1}$); A/Q_{leaf} – ratio of photosynthesis to incident radiation on the leaf ((μmol CO_2 m^{-2} s^{-1})(μmol photons m^{-2} s^{-1})$^{-1}$); A/C_i – instantaneous carboxylation efficiency ((μmol CO_2 m^{-2} s^{-1}) (μmol CO_2 mol^{-1})$^{-1}$); A/g_s – intrinsic water use efficiency ((μmol CO_2 m^{-2} s^{-1})(mol H_2O m^{-2} s^{-1})$^{-1}$); CV: coefficient of variation.

Table 3. Physiological characteristics evaluated in five accessions of umbu trees at different times of reading between Dec 02, 2020 and May 27, 2021 - Guanambi, BA

Variables	Dec 02	Dec 23	Jan 19	Feb 12	Apr 14	Apr 27	May 27	Means	CV (%)
Q_{leaf}	1630.97A	1368.98 B	1781.60A	1085.97 B	1078.62 B	1106.10 B	1624.08AB	1381.87	32.79
T_{leaf}	42.5AB	38.6 B	44.7A	39.9 B	36.2 B	35.7 BC	39.9 B	39.7	11.30
C_i	329.90AB	296.13 C	335.33 B	231.52 D	393.42[a]	299.97 C	352.27AB	319.84	28.82
E	12.81A	3.68 C	11.05A	4.69 BC	0.83 D	5.95 B	2.05 D	5.86	86.92
g_s	0.7223A	0.2105 C	0.3463 B	0.1447 C	0.0305 D	0.5400AB	0.0588 D	0.29	105.62
A	8.09 B	8.00 B	3.50 C	5.97 BC	1.02 C	15.01A	2.91 C	6.35	100.80
WUE	0.9186 B	2.0232A	0.5967 B	1.1934 B	0.6986 B	2.6434A	0.5413 B	1.23	123.12
A/Q_{leaf}	0.0050 B	0.0060 B	0.0018 C	0.0095 B	0.0013 C	0.0149A	0.0018 C	0.0058	123.67
A/C_i	0.0256 B	0.0266 B	0.0140 BC	0.0268 BC	0.0039 C	0.0502A	0.0110 C	0.0225	95.24
A/g_s	16.95 C	47.90A	15.29 BC	44.51A	18.94 B	32.41 B	27.79 B	29.10	117.61

Means followed by same letters do not differ by the Kruskal-Wallis test at 5% significance. Q_{leaf} – incident radiation on the leaf (μmol photons m^{-2} s^{-1}); T_{leaf} – leaf temperature (°C); C_i – internal CO_2 concentration (μmol CO_2 mol^{-1}); E – transpiration (mmol H_2O m^{-2} s^{-1}); g_s – stomatal conductance (mol H_2O m^{-2} s^{-1}); A – net photosynthesis (μmol CO_2 m^{-2} s^{-1}); A/E – instantaneous water use efficiency ((μmol CO_2 m^{-2} s^{-1})(mmol H_2O m^{-2} s^{-1})$^{-1}$); A/Q_{leaf} – ratio of photosynthesis to incident radiation on the leaf ((μmol CO_2 m^{-2} s^{-1})(μmol photons m^{-2} s^{-1})$^{-1}$); A/C_i – instantaneous carboxylation efficiency ((μmol CO_2 m^{-2} s^{-1})(μmol CO_2 mol^{-1})$^{-1}$); A/g_s – intrinsic water use efficiency ((μmol CO_2 m^{-2} s^{-1})(mol H_2O m^{-2} s^{-1})$^{-1}$); CV: coefficient of variation.

Table 4. Physiological characteristics evaluated in five accessions of umbuzeiro, at different reading times, and percentage difference between times (Δ) - Guanambi, BA

Variables	8 a.m.	2 p. m.	Mean	CV (%)	Δ (%)
T_{leaf}	37.00 B	42.30A	39.70	11.30	14.32
C_i	296.92 B	342.65A	319.84	28.82	15.40
E	5.26 B	6.47A	5.86	86.92	23.00
g_s	0.3150A	0.2706 B	0.29	105.62	-14.10
A	9.72A	2.97 B	6.35	100.80	-69.44
WUE	1.9998A	0.4586 B	1.23	123.12	-77.07
A/Q_{leaf}	0.0087A	0.0028 B	0.0058	123.67	-67.82
A/C_i	0.0338A	0.0113 B	0.0225	95.25	-66.57
A/g_s	40.02A	18.24 B	29.10	117.61	-54.42

Means followed by same letters do not differ at 5% significance by the Wilcoxon test; Q_{leaf} – incident radiation on the leaf (μmol photons m^{-2} s^{-1}); T_{leaf} – leaf temperature (°C); C_i – internal CO_2 concentration (μmol CO_2 mol^{-1}); E – transpiration (mmol H_2O m^{-2} s^{-1}); g_s – stomatal conductance (mol H_2O m^{-2} s^{-1}); A – net photosynthesis (μmol CO_2 m^{-2} s^{-1}); A/E – instantaneous water use efficiency ((μmol CO_2 m^{-2} s^{-1})(mmol H_2O m^{-2} s^{-1})$^{-1}$); A/Q_{leaf} – ratio of photosynthesis to incident radiation on the leaf ((μmol CO_2 m^{-2} s^{-1})(μmol photons m^{-2} s^{-1})$^{-1}$); A/C_i – instantaneous carboxylation efficiency ((μmol CO_2 m^{-2} s^{-1})(μmol CO_2 mol^{-1})$^{-1}$); A/g_s – intrinsic water use efficiency ((μmol CO_2 m^{-2} s^{-1})(mol H_2O m^{-2} s^{-1})$^{-1}$); CV: coefficient of variation. Δ (8 a.m. - 2 p.m.), represents the percentage change in the physiological variable, when comparing the measurements taken at 8 a.m. and 2 p.m.; (-) represents decreases and (+) increases; CV: coefficient of variation.

advantage because such accessions, such as the BGU-75 and BGU-50 (Donato et al., 2019b; Santos et al., 2020), showed similar net photosynthetic rates (Donato et al., 2022).

The results suggest the association between higher leaf temperature and lower photosynthetic rate. The effect may be associated with enzymatic problems, corroborated by the similar Q_{leaf} between accessions, with an average of 1381.87 μmol photons m^{-2} s^{-1}. Elevated temperatures lead to denaturation of enzymes, protein instability, imbalances in respiration rates, damages to molecular structures, changes in rubisco activity, thus activating photorespiration, which converts carboxylase activity to oxygenase and reduces net photosynthesis (Arantes et al., 2016; Pino et al., 2019; Moore et al., 2021; Donato et al., 2022). However, real proof would require determination of enzymatic kinetics, such as maximum carboxylation rates of ribulose 1,5-bisphosphate carboxylase/oxygenase (rubisco), photosynthetic rate of electron transport, triose phosphate use, daytime respiration, and mesophyll conductance (Shakey et al., 2007).

BRS-68 and BGU-61 accessions have a similar geographical origin, Lontra, and Januária, both in Minas Gerais state; however, BRS-68 showed greater environmental adaptability due to lower T_{leaf} and higher rates of *A*, WUE, A/C_i, A/g_s and A/Q_{leaf}, closely related variables. From these results, it is assumed that they have genetically different adaptation to the environment and higher metabolic conversion capacity (Arantes et al., 2016). This adaptation can be genotypic and identified by the maintenance or not of physiological processes, for example, photosynthesis and transpiration when different accessions are subjected to stressful environmental conditions, although this assumption is controversial. For example, Silva et al. (2009a) classified BRS-68 as more responsive to drought by showing more sensitive stress-signaling response, as the accession expressed a faster stomatal closure compared to BGU-44, BRS-48 and BGU-50, which means a drop of transpiration rate. These results suggest that BRS-68 is less drought tolerant due to anatomical alterations that include reduced stomatal density, stomatal index, stomatal opening (Silva et al., 2009a), lower water potential values (Ψw), and decreases in carbohydrates and amino acids contents in leaves (Silva et al., 2009b).

The influence of reading date on the physiological variables revealed high variation (Table 3). It is verified that umbu accessions exhibited higher Q_{leaf} and T_{leaf} values on 02/12/2021 and 19/01/2021, lower rates of g_s and *E* on 14/04/2021 and 27/05/2021. g_s was greater on 02/12/2020 which did not differ from that recorded on 27/04/2021, and *E* was greater on 02/12/2020 and similar to that on 19/01/2021. C_i was greater on 04/14/2021 which did not differ from those recorded on 02/02/2021 and 05/27/2021, while *A* was greater on 04/27/2021. Photosynthetic rate, WUE, A/Q_{leaf} and A/C_i were higher on 04/27/2022, while A/g_s was higher on 12/23/2020 and similar to the value recorded on 02/12/2020.

The lowest values of *E* and g_s recorded on 04/14/2021 and 05/27/2021, as well as the lowest rates of *A*, A/C_i and A/Q_{leaf} are associated with the highest values of vapor pressure deficit (VPD) recorded on these days, 2.68 kPa on 04/14/2021 and 2.21 kPa on 05/27/2021, and the rise in temperature (Table 2). The difference between the pressure exerted by the current amount of water vapor in air and the maximum pressure of saturated air, for the same temperature associated with low relative humidity, resulted in high VPD values. The VPD values indicate thermal equilibrium between the plant and surrounding environment. VDP influences the regulation of gas exchange and is closely related to soil water deficit, affecting stomatal conductance, photosynthesis, growth, and productivity (Furtak & Nosalewicz, 2022). In addition, the reading dates already characterize the beginning of the dry season in the region and coincide with phenological stages of accentuated senescence and the beginning of leaf abscission in umbu trees, a condition of lower presence and metabolic activity of leaves (Donato et al., 2019b).

Dry and hot conditions induce a decrease in stomatal conductance and transpiration in umbu trees as a mechanism to avoid water loss, which indicates the adaptation of the umbu tree to semi-arid regions. The morphophysiological mechanisms for drought adaptation are senescence and leaf abscission in the dry period, presence of water- and nutrient-storing tubers in the roots, and osmotic adjustment and high stomatal resistance of leaves. The umbu tree has an isohydric behavior with maintenance of high values of leaf water potential and variation in accumulation of solutes due to drought stress (Silva et al., 2009b).

Furthermore, although very low, transpiration was maintained, even during the hottest hours of the day, highlighting the importance of xylopodia in stabilizing the crop's water balance. This behavior can even be related to the fact that the umbu tree, a species with a C3-type carbon fixation mechanism, can respond to environmental conditions by dropping photosynthetic rates under high temperature conditions due to photorespiration (Arantes et al., 2016; Treves et al., 2022).

Therefore, on 12/02/2020 and 01/19/2021, higher Q_{leaf}, T_{leaf}, g_s and E were recorded, which correlated with a decrease in photosynthesis and WUE, particularly on 12/02/2020. Depending on the period, in midsummer in northeastern Brazilian region, it is common to record higher values of solar radiation and temperature (Table 1), which makes transpiration the main strategy for heat exchange in the plant.

However, at that time, rainfall is likely to occur, which justifies the behavior of accessions. Umbu trees respond relatively well even under reasonable conditions of water availability, due to atmospheric changes with variations in temperature and relative humidity during the day. For example, the lowest incident radiation and leaf temperature recorded on 04/27 stand out, demonstrating favorable environmental conditions for better photosynthetic rates, water use efficiency, quantum and instantaneous carboxylation (Sexton et al. al., 2021), which is explained by the occurrence of rainfall (88.5 mm) between 04/19 and 04/23/2021, the period that preceded the reading.

The highest net photosynthetic rate (*A*) was recorded on 04/27, and the lowest value on 04/14, which was similar to the values recorded on 01/19 and 05/27. During the day on 01/19, in the summer, there was an increase in temperature that differed from the other days evaluated, a favorable condition for stomatal closure to avoid water loss. On these days, there was an increase in VPD and a reduction in relative humidity, which, associated with increased radiation (Table 1), favored a reduction in g_s, which consequently affected photosynthesis (Ramos et al., 2018; Shoa et al. al., 2021).

Umbu trees under these climatic conditions tend to increase the demand for evapotranspiration, which affects metabolic and physiological processes of the plant, which can be perceived by the variations in physiological characteristics, depending on the day of evaluation and the time of reading. Meanwhile, the lowest value was obtained on 04/27, in milder meteorological conditions, with lower VPD and greater water availability due to rains that preceded the day of evaluation, that is, conditions that induce greater conversion of substrate into net photosynthesis.

Subsequently, the high VPD of the atmosphere on 04/14 provided stomatal closure and consequent increase in internal CO_2 concentration values, similar to those recorded on 12/02 and 05/27, while the lowest value was observed on 02/12. Consequently, there was a decrease in photosynthetic efficiency, presuming that the plant decreased carboxylation activity and began to oxygenate; hypothesis confirmed by observing the low rates of net photosynthesis during this period (Santos et al., 2021). Conversely, the highest WUE and A/C_i rates were recorded on 12/23/2020 and 04/27/2021, justified by the occurrence of rainfall in the period prior to the day of evaluation, 18.13 mm on 12/20/2020 and 88.5 mm between 04/19 and 23/04/2021. Rain events improved water availability in soil and contributed to a milder atmosphere with lower VPD because both WUE and A/C_i vary inversely with VPD for the umbu accessions (Donato et al., 2022).

The better environmental conditions in the morning caused plants to express higher metabolic activity owing to better light quality, milder temperatures, higher relative humidity and, consequently, lower VPD, which results in higher g_s values and higher photosynthetic rates, WUE, A/Q_{leaf}, A/C_i, and A/g_s (Table 4). On the other hand, afternoon evaluations (2 p.m.) showed higher values of T_{leaf}, C_i and high E rates, suggesting an efficient defense mechanism of the plant against thermal stress at that moment, when using latent heat loss. Also, the higher internal CO_2 concentration in the afternoon may indicate lower instantaneous rubisco carboxylation efficiency, attested with a low value for this variable (Santos et al., 2021).

Net photosynthesis (A) values were significantly higher in the morning, as well as for WUE, whose reduction between reading times is due to increase in leaf temperature and air temperature. This condition contributed to higher VPD in the afternoon and increased transpiration rates, which is related to the plant's heat exchange mechanism to reduce thermal stress, even with a reduction in stomatal conductance (Arantes et al., 2016; Coelho et al., 2021). There may be no correlation between stomatal conductance and transpiration with VPD in umbu trees (Donato et al., 2022). The measurements reflect the transient limitation of gas exchange, as the measurements taken using IRGA are punctual (Arantes et al., 2016; Ramos et al., 2018).

The reduction in instantaneous carboxylation efficiency and photosynthesis is supposedly due to the increase in leaf temperature, resulting from high air temperature, which leads to an increase in photorespiration rates, functional impairment of membranes, and restriction in rubisco carboxylase activity, thereby reducing ATP synthesis and net photosynthetic rates. This behavior can also be explained by the quality of radiation during the afternoon, which implies a greater amount of unusable energy, which favors non-

Table 5. Correlations between physiological variables in five accessions of umbu accessions - Guanambi, BA

Variables	Q_{leaf}	T_{leaf}	C_i	E	g_s	A	WUE	A/Q_{leaf}	A/C_i	A/g_s
Q_{leaf}	–	0.5110**	0.2794**	0.2754**	0.0870*	-0.1157**	-0.28068*	-0.1765**	-0.1068*	-0.2487**
T_{leaf}		–	0.3099**	0.5840**	0.1815**	-0.5024**	-0.6686**	-0.4047**	-0.3388**	-0.4931**
Ci			–	-0.0101^{ns}	-0.0109^{ns}	-0.3890**	-0.6672**	-0.5968**	-0.4797**	-0.8635**
E				–	0.7999**	0.0958*	-0.1863**	-0.0557^{ns}	-0.0414^{ns}	-0.2786**
g_s					–	0.4447**	0.0415^{ns}	0.1097*	0.0817*	-0.2068**
A						–	0.6125**	0.5182**	0.4192**	0.3427**
WUE							–	0.6102**	0.5062**	0.7336**
A/Q_{leaf}								–	0.5496**	0.6635**
A/C_i									–	0.5259**
A/g_s										–

Q_{leaf} – solar radiation incident on the leaf; T_{leaf} – leaf temperature; C_i – internal CO_2 concentration; E – transpiration; g_s – stomatal conductance; A – net photosynthesis; WUE – instantaneous water use efficiency; A/Q_{leaf} – ratio of photosynthesis to incident radiation on the leaf; A/C_i – instantaneous carboxylation efficiency; A/g_s – intrinsic water use efficiency; **significant at 1%, *significant at 5% by t-test; ^{ns} nonsignificant.

Table 6. Correlations between physiological variables measured in five umbu for two reading times, 8 a.m. and 2 p.m. - Guanambi, BA

Variables	Time 1 (8 a.m.)							
	Q_{leaf}	T_{leaf}	C_i	g_s	A/E	A/Q_{leaf}	A/C_i	A/g_s
C_i	0.0807*	-0.0103 ^{ns}	–	0.2627**	-0.3126	-0.305**	-0.4429**	-0.7061**
E	0.3356**	0.6727**	0.0057 ^{ns}	0.7200**	-0.2980**	0.2894**	0.5319**	-0.5265**
g_s	0.0395 ^{ns}	0.1197**	0.2627**	–	0.0636*	0.4587**	0.6037**	-0.6269**
A	0.0922*	0.0429 ^{ns}	-0.1926**	0.7572**	0.4511**	0.5957**	0.9561**	-0.1759**
Variables	Time 2 (2 p.m.)							
	Q_{leaf}	T_{leaf}	C_i	g_s	A/E	A/Q_{leaf}	A/C_i	A/g_s
C_i	0.4134**	0.2761**	–	-0.0517*	-0.7070**	-0.5912**	-0.4573**	-0.8796**
E	0.2831**	0.6622**	-0.0481^{ns}	0.8685**	-0.1159**	-0.0179 ^{ns}	-0.0058 ^{ns}	-0.204**
g_s	0.1357**	0.3701**	-0.0517*	–	-0.0123 ^{ns}	0.1099**	0.0721*	-0.1317**
A	-0.3134**	-0.4797**	-0.3817**	0.3136**	0.5124**	0.5561**	0.4024**	0.3791**

Q_{leaf} – solar radiation incident on the leaf; T_{leaf} – leaf temperature; C_i – internal CO_2 concentration; E – transpiration; g_s – stomatal conductance; A – net photosynthesis; WUE – instantaneous water use efficiency; A/Q_{leaf} – ratio of photosynthesis to incident radiation on the leaf; A/C_i – instantaneous carboxylation efficiency; A/g_s – intrinsic water use efficiency; **significant at 1%, *significant at 5% by t-test; ^{ns} nonsignificant.

photochemical quenching (Furtak & Nosalewicz, 2022).

The predominant radiation at 8 a.m. has a wavelength in the red and far-red range, which tends to favor the photosynthetic process; on the other hand, radiation at 10 a.m. predominantly has higher energy, potentially causing photoinhibition (Arantes et al., 2016). Clear evidence of the change in radiation quality is that, for the same Q_{leaf} at 8 a.m. and 2 p.m., data not shown because they are statistically similar, the variable with the highest percentage decrease was A/Q_{leaf}. The decreasing order of percentage decrease between times was A/Q_{leaf}, A/C_i, WUE, A/g_s, A and g_s showing greater reductions in efficiencies compared to rates.

The relationships between g_s and E, WUE, A/g_s were positive, significant and of high magnitude (**Table 5**). The opposite occurs with the correlation between C_i and A/g_s which was negative, significant and of high magnitude.

The relationships were similar for both reading times (**Table 6**) positive for variables E and g_s, and negative between C_i and A/g_s. At 8 a.m., significant, high-magnitude, positive correlations were observed between A and A/C_i and between A and g_s; with opposite behavior in the afternoon. However, in the evaluation carried out at 2 p.m., a significant negative correlation of high magnitude was observed between C_i and WUE.

For each pair of variables, between the accessions, there is a difference relative to the magnitude of the correlations in the accessions (**Table 7**). For the relationship between leaf transpiration and stomatal conductance, the values stand out as significant, positive and of high magnitude in the accessions. For the relationship between C_i and A/g_s, significant, negative and high magnitude values were recorded.

Only the correlation in BRS-68 accession was positive, significant and of high magnitude for the association between A and A/C_i. Similarly, Donato et al. (2022), reported among the evaluated accessions, BRS-68 was the only one to maintain the rates of A, A/C_i and WUE with positive values, despite all rates varying negatively with the increase in VPD. As certain characteristics related to productivity, precocity and fruit quality vary according to the interaction between environment and genotype, it is suggested that this accession tends to express greater productive and adaptive capacity to the environment.

Table 7. Correlations between physiological variables of five umbu accessions - Guanambi, BA

Variables	BRS-68							
	Q_{leaf}	T_{leaf}	C_i	g_s	A/E	A/Q_{leaf}	A/C_i	A/g_s
A	0.2229**	-0.2822**	-0.0704*	0.5541**	0.4434**	0.5443**	0.9721**	-0.0436^{ns}
C_i	0.1563**	0.0734*	-	0.4000**	-0.2152**	-0.1715**	-0.2689**	-0.6977**
E	0.2696**	0.6522**	0.2077**	0.8514**	-0.5450**	0.1921**	0.2362**	-0.6421**
g_s	0.1616**	0.2553**	0.4000**	-	-0.2366**	0.3746**	0.4453**	-0.6468**

Variables	EPAMIG-05							
	Q_{leaf}	T_{leaf}	C_i	g_s	A/E	A/Q_{leaf}	A/C_i	A/g_s
A	0.1925**	-0.4794**	-0.3983**	0.2554**	0.7607**	0.3805	0.2516**	0.2204**
C_i	0.0384^{ns}	0.3515**	-	0.4737**	-0.5416**	-0.4231**	-0.2736**	-0.8080**
E	0.4943**	0.7729**	0.4493**	0.8517**	-0.5011**	-0.5460**	-0.3496**	-0.7078**
g_s	0.2798**	0.4169**	0.4737**	-	-0.1790**	-0.3857**	-0.2840**	-0.7154**

Variables	BGU-61							
	Q_{leaf}	T_{leaf}	C_i	g_s	A/E	A/Q_{leaf}	A/C_i	A/g_s
A	-0.3208**	-0.5821**	-0.4028**	0.3586**	0.6318**	0.5188**	0.5273**	0.4373**
C_i	0.4827**	0.4000**	-	-0.1945**	-0.7205**	-0.5893**	-0.2016**	-0.8993**
E	0.1827**	0.5368**	-0.2446**	0.8359**	-0.0064^{ns}	0.1151**	-0.2379**	0.0645*
g_s	0.0375^{ns}	0.2064**	-0.1945**	-	0.0848*	0.1843**	0.0533*	0.0771*

Variables	BGU-75							
	Q_{leaf}	T_{leaf}	C_i	g_s	A/E	A/Q_{leaf}	A/C_i	A/g_s
A	-0.2298**	-0.5537**	-0.4073**	0.7573**	0.6617**	0.5518**	0.3805**	0.3145**
C_i	0.2961**	0.2021**	-	-0.1555**	-0.5695**	-0.6322**	-0.7978**	-0.9056**
E	0.2075**	0.4272**	-0.1658**	0.6976**	-0.0904*	0.0575*	0.3341**	-0.1291**
g_s	0.0085^{ns}	-0.1407**	-0.1555**	-	0.3320**	0.2922**	0.3231**	-0.0619*

Variables	BGU-50							
	Q_{leaf}	T_{leaf}	C_i	g_s	A/E	A/Q_{leaf}	A/C_i	A/g_s
A	-0.2744**	-0.5324**	-0.5535**	0.5108**	0.7909**	0.6576**	0.6633**	0.4393**
C_i	0.2852**	0.3145**	-	0.0355^{ns}	-0.7761**	-0.7216**	-0.8413**	-0.9303**
E	0.2743**	0.5733**	0.1962**	0.8445**	-0.1471**	-0.1781**	-0.0130^{ns}	-0.3656**
g_s	0.0911*	0.1679**	0.0355^{ns}	-	0.1848**	0.1344**	0.2260**	-0.1831**

Q_{leaf} – solar radiation incident on the leaf; T_{leaf} – leaf temperature; C_i – internal CO_2 concentration; E – transpiration; g_s – stomatal conductance; A – net photosynthesis; WUE – instantaneous water use efficiency; A/Q_{leaf} – ratio of photosynthesis to incident radiation on the leaf; A/C_i – instantaneous carboxylation efficiency; A/g_s – intrinsic water use efficiency; **significant at 1%, *significant at 5% by t-test; ^{ns} nonsignificant.

Conclusions

Lower leaf temperatures recorded in BRS-68 and EPAMIG 05 accessions favor higher rates of net photosynthesis, water use efficiency and instantaneous carboxylation efficiency compared to BGU 61.

Umbu tree limits transpiration by reducing stomatal conductance under high vapor pressure deficit, although it increases transpiration as a defense strategy against heat stress, even with reduced stomatal conductance.

High temperature limits instantaneous carboxylation efficiency, photosynthesis and the ratio of photosynthesis to incident radiation on the leaf.

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