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Plant Physiology/ Scientific Notes

Photosynthetic response of umbu trees to vapor pressure deficit

Abstract – The objective of this work was to evaluate the photosynthetic response to vapor pressure deficit (VPD) in umbu (*Spondias tuberosa*) tree accessions. The experiment was carried out in a completely randomized design in a 5×7×2 factorial arrangement (five umbu accessions – BRS-68, EPAMIG-05, BGU-61, BGU-75, and BGU-50 –, seven evaluation times, and two reading times – at 8 a.m. and 2 p.m.) in split-split plots in time. Leaf temperature increased with air temperature. The variation of stomatal conductance and transpiration with the VPD was not significant. Net photosynthesis rate, carboxylation efficiency, and instantaneous water-use efficiency decreased with increasing VPD in all accessions, except in BRS-68, whose rates remained positive.

Index terms: *Spondias tuberosa*, carboxylation efficiency, correlation, ecophysiology, giant umbu.

Resposta fotossintética de umbuzeiro ao deficit de pressão de vapor

Resumo – O objetivo deste trabalho foi avaliar a resposta fotossintética ao deficit de pressão de vapor (DPV) em acessos de umbuzeiro (*Spondias tuberosa*). O experimento foi conduzido em delineamento experimental inteiramente casualizado, em arranjo fatorial 5×7×2 (cinco acessos de umbuzeiro – BRS-68, EPAMIG-05, BGU-61, BGU-75 e BGU-50 –, sete épocas de avaliação e dois momentos de leitura – às 8h e às 14h), em parcelas subsubdivididas no tempo. A temperatura foliar aumentou com a temperatura do ar. A variação da condutância estomática e da transpiração com o DPV não foi significativa. A fotossíntese líquida, a eficiência de carboxilação e a eficiência instantânea do uso da água decresceram com o aumento do DPV em todos os acessos, exceto no BRS-68, cujas taxas se mantiveram positivas.

Termos para indexação: *Spondias tuberosa*, eficiência de carboxilação, correlação, ecofisiologia, umbu-gigante.

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Umbu tree (*Spondias tuberosa* Arruda Câmara) is a fruit tree native to the Caatinga biome, in the Northeast Brazil, which has morphological and physiological adaptations to water deficit conditions (Lima Filho et al., 2008). These adaptations include senescence and leaf abscission during the dry season, the presence of water- and nutrient-storing root tubers, osmotic adjustment, and leaves with high stomatal resistance.

Umbu tree importance has been growing, thereby increasing the demand for information on several aspects associated with this tree, especially on its physiology (Silva et al., 2009; Donato et al., 2019a; Santos et al., 2020).

Physiological measurements in umbu tree accessions allow of the identification of genetic and environmental influences on the development of the tree (Santos et al., 2020). An important environmental factor regulating leaf gas exchange in plants is the vapor pressure deficit (VPD) which, in association with soil moisture deficit, affects their stomatal conductance, photosynthesis, growth, and yield (Lima et al., 2015). Vapor pressure deficit – defined as the difference between the pressure exerted by the amount of moisture in the air and the maximum pressure of water-saturated air – integrates temperature and relative humidity. Due to its influence on the photosynthesis, many authors have established relationships between VPD and gas exchange for several plants (Habermann et al., 2003; McAdam & Brodribb, 2015; Lima Filho & Aidar, 2016).

Understanding how VPD affects gas exchanges in umbu tree accessions can help technicians and growers with the managing of the crop.

The objective of this work was to evaluate the photosynthesis response of umbu tree accessions to the vapor pressure deficit.

The experiment was carried out at the Instituto Federal Baiano, Campus Guanambi, in the state of Bahia, Brazil (14º17'32"S, 42º41'34"W, at 547 m altitude). The soil of the area is classified as a Latossolo Vermelho-Amarelo, according to the Brazilian Soil Classification System (Santos et al., 2018), i.e., Oxisol. The predominant climate in the region, according to the Köppen-Geiger classification, is a hot and dry semiarid, with 25.9°C and 664.7 mm annual means of temperature and rainfall, respectively, based on the average of the past 39 years.

The experiment was carried out in a completely randomized design with treatments arranged in split-split plots and three replicates. Five accessions from two different Brazilian states were assigned to the plots: BRS-68 (EPAMIG-01), EPAMIG-05, and BGU-61, from the municipalities of Lontra, Porteirinha, and Januária, in the state of Minas Gerais, respectively; and BGU-75 and BGU-50, from the municipalities of Macaúbas and Santana, in the state of Bahia, respectively. Seven evaluation periods (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 (8 a.m. and 2 p.m.) were assigned to the subplots and the sub-subplots, respectively.

In the orchard, trees were arranged in a quincunx pattern, 8×8×8 m, and were 13 years old at the time of measurement. Crop practices used in the orchard followed Donato et al. (2019b).

Measurements took place from the rainy season until the beginning of the dry season (December to May). The following parameters were determined: leaf temperature (T_{leaf}, in ºC); stomatal conductance (g_s, in mol H_2O m^{-2} s^{-1}), transpiration (E, in mmol H_2O m^{-2} s^{-1}); net photosynthesis (A, in µmol CO_2 m^{-2} s^{-1}); instantaneous water-use efficiency (WUE, in µmol CO_2 m^{-2} s^{-1} /mmol H_2O m^{-2} s^{-1}); and carboxylation efficiency (A/C_i, in µmol CO_2 m^{-2} s^{-1} /µmol CO_2 mol^{-1}). These parameter were measured using an infrared gas analyzer (IRGA) model Lcpro + Portable Photosynthesis System (ADC BioScientific Limited, UK), at ambient temperature and irradiance, with 200 mL min^{-1} air flow, and a radiation shield facing the sun (Arantes et al., 2016). Readings were carried out on the leaves located in the middle third of the crown, between the 3rd and 5th fully expanded pair of leaves. Air temperature – T_{air} (ºC) and VPD (kPa) were recorded using an automatic weather station at the time of readings. Pearson correlations used T_{leaf} to estimate T_{air}, and VPD to estimate A, A/Ci, and WUE.

For five umbu tree accessions, T_{leaf} increased with air temperature (Table 1). For every 1°C increment of the air temperature, T_{leaf} increased by 0.57°C for EPAMIG-05, 0.61°C for BGU-50, 0.75°C for BRS-68 and BGU-75, and 0.79°C for BGU-61. All correlations were significant, as the accessions originating from the state of Minas Gerais, EPAMIG-05 and BGU-61, showed lower and higher increments in T_{air} with T_{leaf}, respectively, while the accessions bearing heavier fruit, BRS-68 and BGU-75, had similar increments.

Net photosynthesis rate (A) decreased with increasing VPD, for all five umbu tree accessions (Table 1). This is understandable, since the higher is the VPD, the drier is the air. This condition leads to an increase of the stomatal resistance, thereby preventing water loss and restricting the entry of CO_2 (Lima Filho et al., 2008). Decreases of A rates, down to negative values, were recorded on all accessions, except for BRS-68, which showed a lower decrease of A rates (-4.224983 µmol CO_2 m^{-2} s^{-1}) for every kilopascal of VPD. Lima Filho & Aidar (2016) inferred that the accession bearing heavier

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fruit has greater photosynthetic potential; however, the same outcome was not observed in the accession with giant fruit, BGU-75, which may suggest that the greater photosynthesis capacity is a competitive advantage of the BRS-68 accession.

Carboxylation efficiency (A/Ci) decreased with increasing VPD (Table 1). As recorded for photosynthesis, A/Ci reached negative values, except for the BRS-68 accession, on which the smallest decline of A/Ci was recorded (-0.1546 μmol CO_2 m^{-2} s^{-1} /μmol CO_2 mol^{-1} kPa^{-1} of VPD). This means that Rubisco – the enzyme responsible for fixing CO_2 in C3 plants such as the umbu tree – maintained a higher carboxylation rate in BRS-68, with an increase of the VPD, while for the other accessions, the enzyme oxygenase activity intensified the photorespiration.

Table 1. Correlations between leaf temperature and air temperature, and between photosynthesis rate, carboxylation efficiency, and water-use efficiency with vapor pressure deficit for five umbu tree (*Spondias tuberosa*) accessions.

Accession	Correlation	Correlation coefficient
Leaf temperature - T_{leaf} (°C) and air temperature - T_{air} (°C)		
BRS-68	$\hat{T}_{Leaf}$ = 16.16521 + 0.75475Tair	0.575*
EPAMIG-05	$\hat{T}_{Leaf}$ = 22.37378 + 0.57752Tair	0.498*
BGU-61	$\hat{T}_{Leaf}$ = 17.30569 + 0.79967Tair	0.601*
BGU-75	$\hat{T}_{Leaf}$ = 18.52477 + 0.75895Tair	0.598*
BGU-50	$\hat{T}_{Leaf}$ = 22.51507 + 0.61661Tair	0.506*
Photosynthesis rate - A (μmol CO_2 m^{-2} s^{-1}) and vapor pressure deficit - VPD (kPa)		
BRS-68	$\hat{A}$=13.99501-4.22483VPD	-0.701*
EPAMIG-05	$\hat{A}$=16.62090-6.65729VPD	-0.746**
BGU-61	$\hat{A}$=13.98097-5.661821VPD	-0.568*
BGU-75	$\hat{A}$=14.99233-6.01194VPD	-0.657**
BGU-50	$\hat{A}$=15.70150-6.56296VPD	-0.595*
Carboxylation efficiency – A/C_i (μmol CO_2 m^{-2} s^{-1}/μmol CO_2 mol^{-1})		
BRS-68	$\widehat{A/C_i}$=0.01546-0.01546VPD	-0.702**
EPAMIG-05	$\widehat{A/C_i}$=0.06046-0.02426VPD	-0.738**
BGU-61	$\widehat{A/C_i}$=0.04673-0.01846VPD	-0.571*
BGU-75	$\widehat{A/C_i}$=0.04981-0.01957VPD	-0.662*
BGU-50	$\widehat{A/C_i}$=0.05203-0.02046VPD	-0.601*
Water-use efficiency – WUE (μmol CO_2 m^{-2} s^{-1}/mmol H_2O m^{-2} s^{-1}) and vapor pressure deficit - VPD (kPa)		
BRS-68	$\widehat{WUE}$ =3.44816-0.89762VPD	-0.514*
EPAMIG-05	$\widehat{WUE}$ =2.86952-0.85643VPD	-0.698**
BGU-61	$\widehat{WUE}$ =3.45356-1.94132VPD	-0.682**
BGU-75	$\widehat{WUE}$ =2.74730-1.23844VPD	-0.685**
BGU-50	$\widehat{WUE}$ =2.73392-1.14338VPD	-0.723**

**,*Significant at 1% and 5%, respectively, by the t-test.

Decreases of the photosynthesis rates result from the stomatal resistance increase that restricts the entry of CO_2 and from the increase of Rubisco oxygenase activity with an increase of VPD, which implies high temperature and low relative humidity (Lima Filho & Aidar, 2016).

Instantaneous water-use efficiency (WUE) – the ratio between photosynthesis and transpiration (A/E) – decreased with increasing VPD, as well as A and A/Ci (Table 1). Similarly, the only accession that kept WUE at positive rates with the increase of VPD was BRS-68 which, together with EPAMIG-05, expressed the lowest decreases of WUE per unit of VPD. These results corroborate those by Silva et al. (2009), who reported lower transpiration values for BRS-68 under optimal soil moisture conditions, as WUE is inversely proportional to E, and it varies proportionally with A. These authors also found a greater drought responsiveness for this accession because it exhibited faster stomatal closure. Therefore, it appears that BRS-68 maintains a higher photosynthesis and lower transpiration rates under conditions of high VPD, in comparison with other accessions, due to its greater stomatal control and Rubisco carboxylase activity.

The variation of stomatal conductance with the VPD was random (Table 2). Most correlations were nonsignificant, of very low magnitude, and negative.

Table 2. Correlations between stomatal conductance and transpiration rate with vapor pressure deficit for five umbu (*Spondias tuberosa*) tree accessions.

Accession	Correlation	Correlation coefficient
Stomatal conductance - g_s (mol H_2O m^{-2} s^{-1}) and vapor pressure deficit - VPD (kPa)		
BRS-68	$\hat{g}_s$=0.27139-0.03974VPD	-0.175^{ns}
EPAMIG-05	$\hat{g}_s$=0.31537-0.03039VPD	-0.087^{ns}
BGU-61	$\hat{g}_s$=0.30731+0.033305VPD	0.055^{ns}
BGU-75	$\hat{g}_s$=0.57797-0.18292VPD	-0.406*
BGU-50	$\hat{g}_s$=0.43151-0.07171VPD	-0.154^{ns}
Transpiration rate – E (mmol H_2O m^{-2} s^{-1}) and vapor pressure deficit - VPD (kPa)		
BRS-68	$\hat{E}$=3.94119+0.63071VPD	0.118^{ns}
EPAMIG-05	$\hat{E}$=4.53666+0.78644VPD	0.101^{ns}
BGU-61	$\hat{E}$=4.86618+0.88778VPD	0.105^{ns}
BGU-75	$\hat{E}$=6.91645-0.63685VPD	-0.088^{ns}
BGU-50	$\hat{E}$=6.29799+0.17067VPD	0.023^{ns}

*Significant by the t-test, at 5% probability. ^{ns}Nonsignificant.

Exceptions were recorded for the accession BGU-75 which showed a significant correlation with moderate magnitude, and for the accession BGU-61 which was positive. The correlations between transpiration and VPD were all nonsignificant, without significant magnitude, and positive, except for the accession BGU-75 which was negative.

These results suggest that the greatest effect on photosynthesis was enzymatic, supported by variations of carboxylation efficiency and water-use efficiency (Table 1), despiste fateful claims about rubisco carboxylation efficiency demand determination of the enzyme kinetic parameters, such as maximum carboxylation rate of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco), photosynthetic rate of electron transport, use of triose phosphate, daytime respiration and mesophyll conductance (Sharkey et al., 2007). However, these parameters require measurements adjusted at 25°C to facilitate the comparison, and this work was carried out at room temperature.

Leaf temperature increases with increasing air temperature, while net photosynthesis rates, carboxylation efficiency and instantaneous water-use efficiency decrease at increasing vapor pressure deficit, in all umbu tree accessions; however, the accession BRS-68 (EPAMIG-01) maintains these rates at positive values, which suggests its greater adaptation to conditions of high vapor pressure deficit.

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