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ORIGINAL ARTICLE

Physiological assessment in young Brazilian and African mahogany plants during the dry and rainy seasons in northeastern Para state, Brazil

Fisiologia de plantas jovens de mogno brasileiro e africano nas épocas chuvosa e seca no Nordeste paraense

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ABSTRACT: Because of their high commercial value and international market acceptance, mahogany species have been indiscriminately explored even in protected areas, resulting in extinction threat. In this study, we aimed to assess the physiology of young plants of Brazilian (*Swietenia macrophylla* (King)) and African (*Khaya ivorensis* A. Chev.) mahogany regarding their drought tolerance. The species analyzed showed different responses in the behavior of variables in the two periods studied. The highest values of stomatal conductance (*gs*) and transpiration (*E*) were observed in the rainy season because of excess of soil water; while in the dry season, deficit of soil water caused *gs* reduction of 90% in 2006 and 75% in 2007, and *E* reduction of 80% and 60%, respectively, for the same periods. The dry season, with lower values of leaf water potential and leaf relative water content, induced higher levels of sucrose, proline and total soluble amino acids compared to the rainy season, indicating emergence of the mechanism of osmoregulation in the studied species.

RESUMO: *As espécies de mogno, por seu alto valor comercial e aceitação no mercado internacional, têm sido exploradas de forma indiscriminada, mesmo em áreas protegidas, acarretando ameaça de extinção. O objetivo deste trabalho foi estudar a fisiologia de plantas jovens de mogno brasileiro [Swietenia macrophylla (King)] e africano (Khaya ivorensis A. Chev.) quanto à tolerância à seca. As espécies apresentaram diferentes respostas no comportamento das variáveis, nas duas épocas estudadas. Os maiores valores de condutância estomática (gs) e transpiração (E) foram observados na época chuvosa, em virtude do excedente hídrico do solo, enquanto que, na época seca, a deficiência hídrica promoveu redução de gs em 90%, em 2006, e em 75%, em 2007; de E, observaram-se valores de 80% e de 60%, respectivamente, no mesmo período. O período seco, com menores valores de potencial hídrico foliar e do conteúdo relativo de água na folha, induziu maiores teores de sacarose, prolina e aminoácidos solúveis totais, em comparação ao período chuvoso, apontando para o surgimento do mecanismo de osmorregulação nas espécies estudadas.*

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1 Introduction

Brazilian (*Swietenia macrophylla* (King)) and African (*Khaya ivorensis* (A. Chev.)) mahogany species have been used in the Amazon region associated with agroforestry, silvopastoral activities, or even in homogeneous crops for export. Many of the crops associated with these species are located in areas subject to water stress resulting from uneven rainfall distribution, where the occurrence of six-month long dry periods with monthly rainfall below 100 mm is rather common. Under these field conditions, newly installed plants may undergo severe water stress caused by high levels of incident radiation, and may undergo major loss of water (CARVALHO, 2005).

Periodic monitoring of seasonal and diurnal variations of leaf water potential, and of gas exchange when combined with measurements of stomatal conductance and climatic variations, may serve as important tools for understanding how a particular species uses available resources from the environment and how seasonal fluctuations of these resources affect the primary productivity of plants. Thus, assessment of the effects caused by the dry season is of great importance not only with a view to economic production, but also when trying to clarify how and in what proportions these parameters may contribute to survival during such periods (DAMATTA et al., 2003).

Stomatal movement is the primary control mechanism of gas exchange in terrestrial higher plants and its operation constitutes a physiological impairment: open stomata, allow the absorption of CO_2; closed stomata, conserve water and reduce the risk of dehydration. As soil water availability decreases, transpiration rate decreases as a result of stomatal closure, which constitutes an important defense mechanism of plants against excessive loss of water and eventual death by desiccation (LARCHER, 2004).

Leaf water potential indicates leaf energy status so that diurnal variations of atmospheric evaporative demand change this status of energy and explain water flow in the soil-plant-atmosphere system (BERGONCI et al., 2000). As the opening/closure stomatal process is related to leaf hydration status, such variations can affect the productivity of plants. In young plants of peach palm, there was a 92% decrease in photosynthesis when leaf water potential fell to -1.9 MPa (OLIVEIRA et al., 2002), showing the strong effect of leaf hydration status on carbon assimilation.

It is known that water stress causes changes in the composition of cells of higher plants, often leading to production of osmotically active organic substances, such as proline, soluble amino acids and soluble carbohydrates (CARVALHO, 2005). This process, known as osmoregulation, is a very important component in the process of drought tolerance in several species (SILVA et al., 2004). We compared the physiological responses of African and Brazilian mahogany young plants in two periods (rainy and dry) and evaluated their drought tolerance.

2 Materials and Methods

This experiment was carried out under field conditions in the municipality of Igarapé Açú, state of Pará (01° 12' S and 47° 36' W) from March 2006 to November 2007. The climatic environment is influenced by the Ami climate type according to Köppen classification, with rainy season between January and July and dry season between September and November. August is considered the transition month between the rainy and dry seasons. Soil was classified as Yellow Latosol, medium texture (EMBRAPA, 2006), with the following physical and chemical attributes (0-20 cm depth): coarse sand 546 g kg^{-1}, fine sand 278 g kg^{-1}, silt 36 g kg^{-1}, total clay 140 g kg^{-1}, phosphorus 3 mg dm^{-3}, potassium 25 mg dm^{-3}, calcium 1.4 mg dm^{-3}, magnesium 1.1 mg dm^{-3}, aluminum 0.6 $cmol_c$ dm^{-3} and pH in water (1:2.5) 5.5.

We used an experimental randomized block design arranged in a 2 x 2 factorial consisting of two species (*S. macrophylla* and *K. ivorensis*) and two hydric conditions (rainy and dry), with eight replicates. Planting occurred in March, when plants were six months old and about 60 cm in height, spaced 4 x 4 m. In 2006 and 2007, each plant received 300 g of lime, 150 g of superphosphate, 100 g of urea and 100 g of potassium chloride.

The averages of air temperature (T_{air}) and relative humidity (RH) were determined using a thermo-hygrometer (model 5203, Incoterm, RS, Brazil); vapor pressure deficit between leaf and atmosphere (VPD_{LA}) was estimated according to Landsberg (1986); photosynthetically active radiation (PAR) was measured using a quantum sensor coupled to a porometer; and rainfall data were provided by a climatological station of 'Embrapa Amazônia Oriental', located in the vicinity of the experimental area. The environmental variables (T_{air}, RH and PAR) were measured between 12-1 pm, weekly over the months of 2006 and 2007.

Stomatal conductance to water vapor (*gs*), transpiration (*E*) and leaf temperature (T_{leaf}) were determined using a dynamic equilibrium portable porometer (model 1600 LiCor, Nebraska, USA) under ambient light and CO2, every month between 12-1 pm, on physiologically active folioles. Leaf water potential (Ψ_{leaf}) was determined between 4-5 am, 12-1 pm and 5-6 pm using a pressure pump (Pms Instrument Co., Corvalles, USA) and relative water content (RWC) was determined between 6-7 am, 12-1 pm and 5-6 pm, according to Slavick (1979). Both (Ψ_{leaf}) and RWC were measured only in 2007 because there was increased fall of leaves in both species during the dry period of 2006.

Sucrose, total soluble amino acids and proline were measured according to Van Handel (1968), Peoples et al. (1989) and Bates, Waldren and Teare (1973), respectively. These measurements were also performed at the end of the rainy and dry seasons of 2007, in mature folioles detached from plants between 12-1 pm, after being dried in a forced ventilation oven at 68 °C for 72 h.

Results were analyzed using the NTIA software program, version 4.2.1. Statistical significance of means of the response variables was assessed by the Tukey test (p <0.05) and variables from the dry and rainy seasons were correlated.

3 Results and Discussion

The means of the environmental variables that were taken for the same period were relatively constant, indicating that determinations of the physiological variables were performed under the same conditions (Figure 1).

The following results were verified in 2006 and 2007: average monthly rainfall of 302.8 mm in the rainy season and 50.2 mm in the dry season (Figure 1A); PAR of 1087.5 μmol m^{-2} s^{-1} in the rainy period and 1822.5 μmol m^{-2} s^{-1} in the dry period (Figure 1B); RH of 70% in the rainy season and 52% during the dry period (Figure 1C); T_{air} and T_{leaf} curves followed the same trend of the Par curve, preserving the magnitudes inherent to each of them, reaching averages of 32.7 °C and 32.5 °C in the rainy season and 35.7 °C and 36.1 °C in the dry season, respectively for 2006 and 2007 (Figures 1D and 1E). Considering the averages observed for T_{air}, T_{leaf} and RH, we calculated the VPD_{LA}, which presented means of 1.7 kPa in the rainy season and 3.3 kPa during the dry period (Figure 1F).

Stomatal conductance (*gs*) and transpiration (*E*) were higher during the rainy season compared to the dry season in

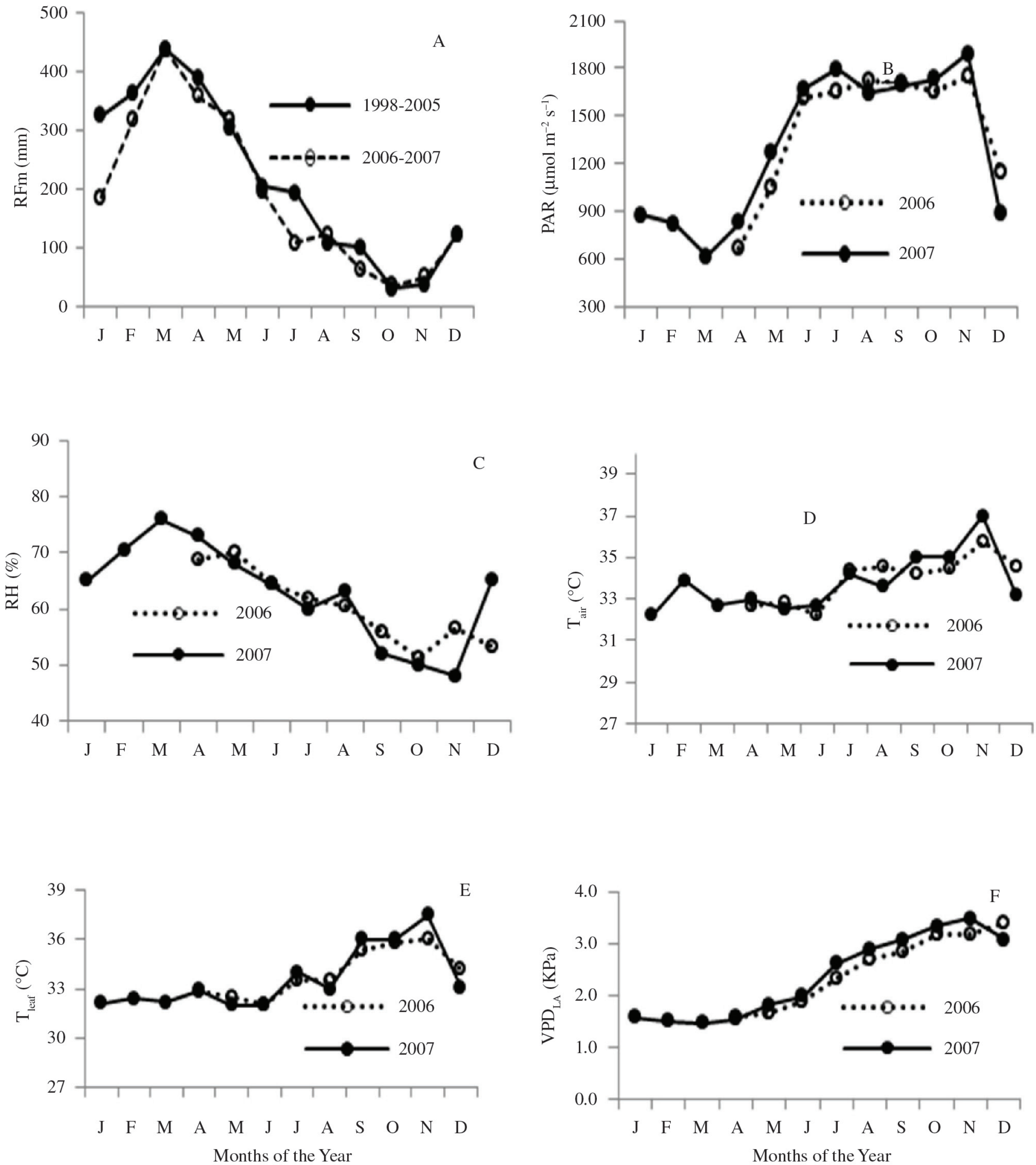

Figure 1. Monthly rainfall (RFm; A), photosynthetically active radiation (PAR; B), relative humidity (RH; C), air temperature (T_{air}; D), leaf temperature (T_{leaf}; E), and vapor pressure deficit between leaf and atmosphere (VPD_{LA}; F) in Brazilian and African mahogany in the rainy and dry seasons.

both species (Figure 2). There was significant reduction in gas exchange with water stress increase. Stomatal closure under water stress conditions was, in fact, the main cause of reduction in transpiration rate: from 80% in 2006 to 60% in 2007. Thus, decreased water availability causes decreased leaf water potential in plants, leading to loss of turgor and hence reduction in stomatal conductance and transpiration (TATAGIBA et al., 2007; TAVARES DE PAULA et al., 2011). Thus, the decrease in gas exchange of African and Brazilian mahogany, with soil water reduction, may be directly associated with a change of the stomatal behavior of these species. Evidence of this nature was mentioned by Costa and Marenco (2007) e Gonçalves, Silva and Guimarães (2009) for *Carapa guianensis* and by Cordeiro et al. (2009) for *S. macrophylla*.

The significant reduction in the transpiration rates in January, February and March 2007 (Figure 2) occurred possibly due to decreased PAR (Figure 1), caused by the high cloudiness that occurred during these months, as well as to the fall of folioles and probable death of shallow roots, caused by the dry season of 2006. Research has shown that the development and growth of roots and shoots are interdependent, that is, the limitation of one, results in restriction to the other. Thus, the defoliation of shoots is followed by considerable death of roots (CASTRO; CATO; VIEIRA, 2001; TAIZ; ZEIGER, 2009).

The higher transpiration rates reached by African mahogany compared to Brazilian mahogany, in the rainy season (Figure 2), should be attributed to the genetic character of this species. In fact, African mahogany differs from Brazilian mahogany in leaf shape and size and canopy architecture. Species showed significant variation in Ψfol and RWC according to the time of day and season (Figure 3).

Throughout the day, the lowest values in Ψfol and RWC were observed between 12-1 pm coinciding with the time of highest evaporative demand (Figure 1F). However, during the dry period, values of RWC and Ψ_{leaf}, at all assessment times, were always lower than the values recorded for plants in the rainy season. The decreases in Ψ_{leaf} from –0.2 MPa at 4-5 am to –1.96 MPa at 12-1 pm and in RWC from 96% to 80%, at the same time, during the rainy season, may be associated with the discrepancy between transpiration and root water uptake rates (MORAIS et al., 2007); whereas, in the dry season, Ψ_{leaf} = –3.01 MPa and RWC = 70% between 12-1 pm may be related to water stress and intracellular accumulation of osmotically active substances (Table 1). Morais et al. (2007) evaluated the daily and seasonal behaviors of leaf water potential in several constituent species of the central

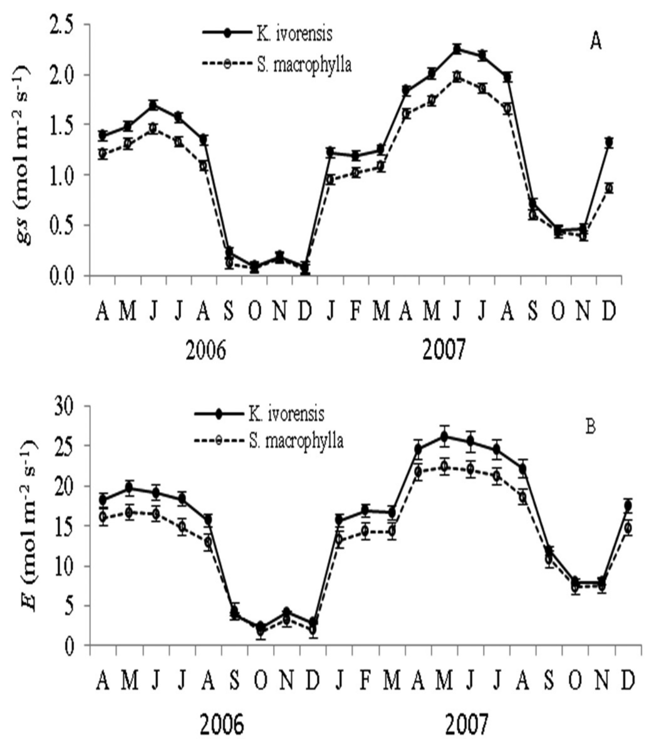

Figure 2. Monthly variation of stomatal conductance (*gs*) (A) and transpiration (*E*) (B) measured between 12-1 pm in leaves of *K. ivorensis* and *S. macrophylla* in the rainy and dry seasons of 2006 and 2007.

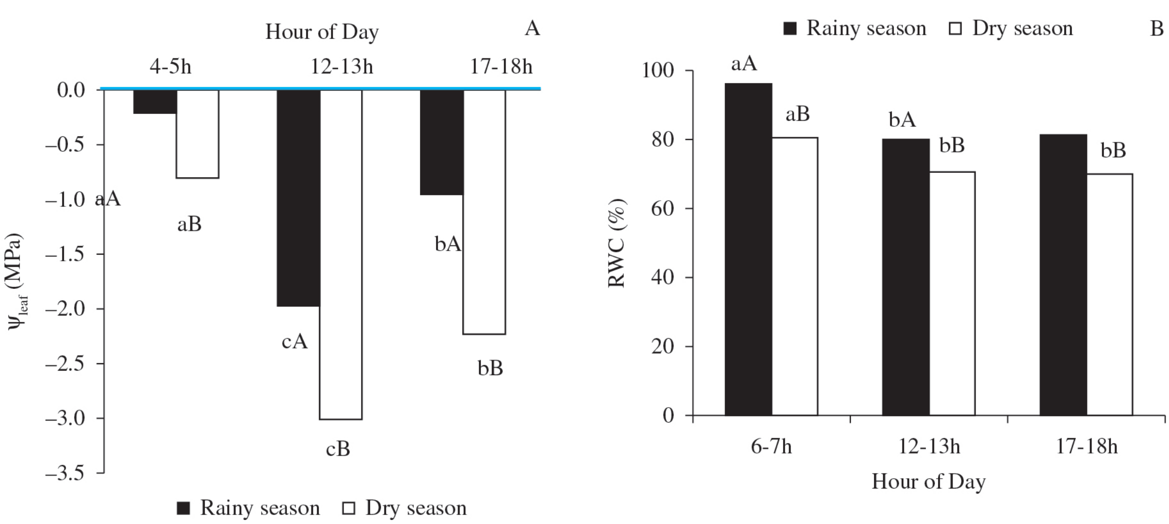

Figure 3. Diurnal leaf water potential (Ψleaf) and relative water content (RWC) in Brazilian and African mahogany plants in the rainy and dry seasons. Lowercase letters compare daylight hours within the same climatic period and uppercase letters compare climatic periods in the same time of day, by the Tukey test (p <0.05).

Table 1. Concentrations of sucrose, proline and total soluble amino acids (TSA) in leaves *of K. ivorensis (Ki)* and *S. macrophylla (Sm)*, in the rainy (RP) and dry (DP) periods of 2007.

Species	Sucrose (g kg^{-1})		Proline (mmol kg^{-1})		AST (g kg^{-1})	
	RP	DP	RP	DP	RP	DP
Ki	14.00 bB	36.08 bA	13.16 aB	85.55 aA	20.12 aB	48.02 aA
Sm	23.06 aB	39.04 aA	7.97 bB	24.82 bA	12.31 bB	26.19 bB
CV	10.96		15.55		6.98	

Lowercase letters compare species and uppercase letters compare periods, by the Tukey test (p <0.05).

Amazon agroforestry system and found that plants showed reduced Ψ_{leaf} throughout the day, more expressively in the dry season; in this period, Ψ_{leaf} values obtained at 12 pm (–3 MPa) and at 5 am (–1 MPa) showed that *S. macrophylla*, among the species studied, presented the lowest values. Reduction in Ψfol and RWC and increase in the levels of osmotically active substances, as plant responses to water deficit, were also observed in *S. macrophylla* by Cordeiro et al. (2009) and in *S. amazonicum* and *S. parahyba* by Carvalho (2005).

Linear correlation analyses show that, except for Ψfol, *gs*, *E* and RWC were more influenced by PAR and VPD_{LA} in the rainy season (Table 2). In contrast, during the dry season, *gs* and *E* were weakly correlated to VPD_{LA}, which is calculated taking into account RH, T_{air} and T_{leaf}, indicating that stomatal closure in the dry period seemed to be more associated with changes in soil water potential than with variations in atmospheric conditions. Tatagiba et al. (2007), when analyzing the behavior of two clones of *Eucalyptus* in the dry and rainy seasons, found that reduction in gas exchange was more closely related to decreased soil moisture, imposed by the dry season, than to environmental factors such as light, temperature and relative humidity.

We verified that the water deficit significantly increased the concentration of osmotically active substances in both species (Table 1). Therefore, *K. ivorensis* accumulated about 2.6 times more sucrose, 6.5 times more proline and 3.4 times more TSA in the dry season compared to the rainy season; while *S. macrophylla* accumulated 1.7 times more sucrose, 3.1 times more proline and 2.1 times more TSA under the same conditions. According to Subbarao, Chauhan and Johansen (2000), accumulation of amino acids and free sugars may occur because of restriction to protein synthesis and to hydrolysis of starch reserves, as well as disorders caused by water stress in phloem tissues, reducing translocation to other organs. These compounds, in addition to providing advantages from the standpoint of lowering the osmotic potential and turgor maintenance, serve as a carbon and nitrogen reserves for immediate growth recovery, because environmental stresses are relieved (SZEGLETES, 2000).

Plants exposed to water stress generally present accumulation of osmotically active substances that have been associated with plant tolerance to this adverse condition, which may represent a regulatory water loss mechanism that operates by increasing cellular osmolarity (CARVALHO, 2005) .

Under water stress conditions several physiological processes are altered, such as photosynthesis, respiration, transpiration, stomatal conductance, abscisic acid production, leaf abscission, and osmotic adjustment (MARIN et al., 2006).

Table 2. Pearson correlation coefficient between stomatal conductance (*gs*), transpiration (*E*), leaf water potential (Ψ_{leaf}), relative water content (RWC), photosynthetically active radiation (PAR), and vapor pressure deficit (VPD_{LA}) in African and Brazilian mahogany plants, during the rainy (PC) and dry (PS) periods of 2007.

Correlations	RP	DP
$gs \times$ VPD	0.83**	–0.18^{ns}
$gs \times VPD_{LA}$	0.77**	–0.65*
$E \times$ VPD	0.91***	0.25^{ns}
$E \times VPD_{LA}$	0.88**	–0.71*
$\Psi_{leaf} \times$ VPD	–0.98***	–0.67^{ns}
$\Psi_{leaf} \times VPD_{LA}$	–0.98***	0.98***
RWC × VPD	–0.93**	0.50^{ns}
RWC × VPD_{LA}	–0.95**	–0.63^{ns}

Notes: ns - no significant; *P < 0.05; **P < 0.01; ***P < 0.001.

Within this context, based on the results obtained in this study, we concluded that the species *K. ivorensis* and *S. macrophylla* presented accumulation of solutes, reflected in decreased leaf osmotic potential as a response to water stress, characterizing a possible osmotic adjustment. This mechanism is probably one of the strategies that, acting in conjunction with other factors, allow species to survive under stressful conditions that occur in their natural environment.

4 Conclusions

In the rainy season, African mahogany showed higher values of transpiration rate and stomatal conductance than Brazilian mahogany.

Gas exchange, relative water content, and contents of organic osmolytes were similarly affected by the dry period in both species

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