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ORIGINAL PAPER

Transpiration and growth of young African mahogany plants subject to different water regimes

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Abstract

Timber production has been prominent in the Brazil scenario to minimize deforestation. Thus, technical information is necessary to define the productive process of the African mahogany in the Midwest region of Brazil, especially with regard to its hydric parameters. Recent studies, reported in the literature, have shown that irrigation improves the performance of young African mahogany plants in the field. Sap flow measurement can be used to estimate transpiration of perennial plants and to determine their water demand. This study evaluated the influence of two water regimes on the transpiration and growth of an African mahogany forest after irrigation has ceased. Moreover, this study also characterizes the seasonal patterns of transpiration and growth of African mahogany under these conditions. African mahogany plants with 2.5 years of age were cultivated in Bonfinopolis-GO and evaluated for 2 years. Treatments were IT—irrigated until 2 years of age—and NIT—non-irrigated. Plant height (PH), breast height diameter (DBH), trunk volume (TRV), leaf area (LA), leaf dry matter (LDM), and transpiration (T) were monitored by heat dissipation probe (HDP) between Oct/2014 and Oct/2015. Higher growth in LA, DBH, and LDM were observed in IT. However, increase in PH and TRV was similar in both treatments. The mean annual T was similar between treatments (15.0 L m^{-2} $month^{-1}$). The highest T was recorded in October/2014 (IT = 33.0 L m^{-2} $month^{-1}$) and July/2015 (NIT = 20.5 L m^{-2} $month^{-1}$). The greater LA and water deficit blades DEF > 30 mm promoted lower transpiration in the irrigated plants. Irrigation maintained plant growth in PH, DBH, and LA in the third year, even after irrigation has ceased. However, non-irrigated plants were similar in TRV (0.065 m^3) and transpiration rates (≈ 15 L m^{-2} $month^{-1}$). Winter transpiration (11.3 L m^{-2} $month^{-1}$) was lower than in summer (18.8 L m^{-2} $month^{-1}$) for irrigated plants and similar for non-irrigated plants (≈ 14 L m^{-2} $month^{-1}$). Based on that, in order to maintain the homogeneity of the plants, the irrigation in the first 2 years of cultivation is recommended, and also, the sap flow measures presented satisfactory results regarding the determinations of the water needs of African mahogany.

Keywords *Khaya ivorensis* A. Chev. · Cultivated forest · Sap flow · Water deficit

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Introduction

Global warming can cause extreme events, such as prolonged periods of drought. Trees are large "water producers" because they allow the connection of deeper soil layers with the atmosphere by generating water dynamics in the soil-plant-atmosphere system (Trabucco et al. 2008; Zomer et al. 2014; Ekhuemelo et al. 2016). Thus, studies describing water relations of tree species are important for both reforestation and timber production aiming at minimizing deforestation. In addition, young African mahogany plants present high stomatal sensitivity to water deficit, making that species tolerant to water stresses moderate (Albuquerque et al. 2013).

Crops of African mahogany (*Khaya ivorensis* A. Chev.) in Brazil were driven by the timber added value and the species adaptation to the country's edaphoclimatic conditions (Casaroli et al. 2018). In addition, that species already has its economic viability proven from Brazilian Savanna studies (Grupioni et al. 2018). The Midwest region has stood out in the last decades for the expansion of agricultural production and variety of exploited crops. Forest crops are used in the recovery of degraded areas and integration systems (Morales et al. 2012). Rainfall is a limiting factor for yield of *K. ivorensis*; however, the seasonality of rainfall in the Midwest region raises doubts about the need for irrigation to meet the water demand of this crop.

The relationship between water availability and forest production is related to the direct and indirect effects of water deficiency on tree growth. Among these effects, the following stand out: decrease of photosynthetic rate due to the increased stomatal resistance, decrease of nutritional potential of the trees through mass flow and diffusion, decreased rate of mineralization of organic matter, water deficiency, and the functional cytoplasmic and tissue collapse itself (Sands and Mulligan 1990; Sacramento Neto 2001; Fuchs et al. 2017).

Crops for timber production can withstand the typical summer of the Midwest region without any damage to the quality of the final product. However, research on the effects of irrigation or lack thereof on crop growth and development is necessary to validate this claim. Some studies on mahogany show higher growth of this species when irrigated in the first 2 years of cultivation (Alves Júnior et al. 2017), besides potential growth under agrometeorological conditions of the Cerrado of Goiás when its water needs are supplied (Casaroli et al. 2016).

The crop water consumption is usually determined by direct methods, such as by lysimetry (Casaroli et al. 2016) or estimated by agrometeorological models of evapotranspiration: Penman-Monteith, Thornthwaite, Hargreaves, among others. It is noteworthy that transpiration measures better characterize the water requirement in discontinuous soil cover as in tree crops than those of evapotranspiration (Vellame et al. 2011; Sérvulo et al. 2017; Padovan et al. 2018). Thus, methods to measure sap flow have been chosen in the estimates of transpiration in perennial plantings because they guarantee better representativeness. Sap flow measurements are a good alternative for determining the water needs of the African mahogany and are based on the influence of the atmosphere evaporative demand on the upward movement of water in the plant, allowing the water monitoring in the tree component of the soil-plant-atmosphere. The estimation of transpiration based on these methodologies presupposes the equivalence between sap flow in the trunk and the transpiratory flow in the foliar surfaces. This assumption is valid when considering flow on a daily scale (Coelho Filho et al. 2005; Delgado-Rojas et al. 2007). The heat dissipation probe method developed by Granier (1987) determines the sap flow density in the stem and allows the estimation of this flow in woody plants. The author related the speed of heat dissipation applied punctually in the trunk with the sap flow density. The temporal variation of temperature difference between this point and a point below is caused by convective transport of heat by the sap. The fact of quantifying only the transpiratory component can be an advantage when measuring water use by the plant, but a disadvantage in projecting total evaporation of a heterogeneous surface (Allen et al. 2011). This study evaluated the influence of two water regimes applied to the implantation of an African mahogany forest on transpiration and growth after irrigation has ceased. Further, the study characterizes seasonal patterns of African mahogany transpiration and growth under those conditions.

Material and methods

Experimental site

The African mahogany forest (*Khaya ivorensis* A. Chev.) was planted in March/2012, using seedlings from seeds from the state of Pará (Brazil). The experiment was carried out in the forest, 5.0 × 5.0 m spaced, located in Bonfinópolis, GO, Brazil (16° 35′33″ S, 49° 01′47″ W, 871 m). According to Köppen's climate classification, the climate is Aw, savanna climate, megathermal with well-defined dry (May–September) and rainy (October–April) seasons (Alvares et al. 2013). The annual mean temperature and annual rainfall are approximately 24 °C and 1400 mm (INMET 2018). The predominant soil is the Cerrado Oxisol, clay texture, Cerradão subperennial stage, flat relief (Embrapa 2013). The granulometric analysis determined for layers of 0.0–0.2 and 0.2–0.4 m, respectively: sand = 38.0% and 47.0%; silt = 24.0% and 23.0%; clay = 38.0% and 30.0% (loamy clay texture).

Data on air temperature (T_a), relative air humidity (RH), incident global solar irradiance (Rs), wind speed (U_2), and rainfall (P) were obtained in the automatic weather station, Vantage Pro2 from Davis® company (Davis® 2018), installed next to the experiment (50 m). The reference evapotranspiration (ET_0) was estimated by Hargreaves and Samani (1985) equation. The vapor pressure deficit (VPD) was calculated from the Ta and RH, using the Tetens equation to determine saturation vapor pressure (e_s). The daily average vapor pressure deficit (VPD_d) was obtained by the average VPD at the 06:00 to 18:00 h interval.

The crop water balance (Thornthwaite and Mather 1955) was in periods divided into months from March/2014 to October/2015. The cultivation coefficient Kc = 1.0 and the available water capacity (AWC) of 300 mm recommended for perennial species were used (Allen et al. 2006).

Treatments and experimental design

Trees were submitted to different water regimes in the first 2 years of age (731 days after planting—DAP). The following treatments were applied: IT—trees irrigated until 2 years of age—and NIT—non-irrigated trees. Six trees of each treatment were evaluated to transpiration and biometric measures. Data collection was initiated at 945 days after planting, when the forest reached approximately 2.5 years of age (Fig. 1).

Treatments were two water regimes, irrigated until 2 years of age and not irrigated. Also, five evaluation times were compared by regression analysis. For the analysis, growth rates were evaluated only four times.

Biometric assessments

Biometric assessments were performed between February and August/2015 (Fig. 1) by measuring plant height (H)—obtained with the aid of electronic forest clinometer (m); diameter at breast height (DBH)—measured with a manual forest cover (m); dry leaf biomass accumulation (LB)—estimated by Eq. [1], expressed in kg (Heryati et al. 2011); trunk volume (TRV)—estimated by Eq. [2] and expressed in m^3 (Heryati et al. 2011):

$$LB = 0.02248 \times DBH^{2.23872} \tag{1}$$

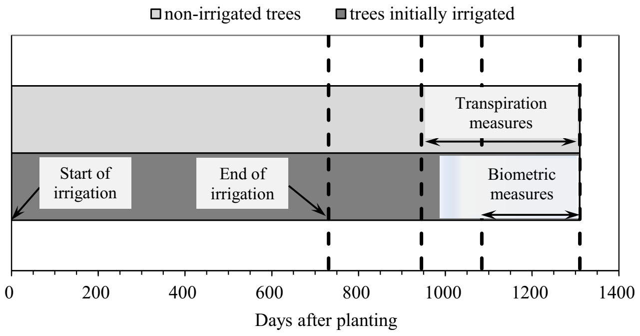

Fig. 1 Temporal representation of evaluations and imposition of treatments. The two treatments were evaluated for both transpiration and biometry

$$TRV = 0.00014 \times \left(DBH^2 \cdot PH\right)^{0.84469} \tag{2}$$

where PH is the tree total height (m). Both equations were tested and validated for *Khaya ivorensis* A. Chev. in this study. All leaves were removed from a tree close to the experimental plots having their leaflet areas measured (LI-COR 3000 integrator). Afterwards, leaflets were dried in a forced ventilation oven (65 °C/48 h) for dry leaf mass. The leaf area (LA, m^2) was estimated by the linear relation with LB, obtaining Eq. [3]:

$$LA = 7.1 \times LB \tag{3}$$

Transpiration by Granier method

Tree transpiration was determined by the Granier method (1987), which is a heat supply to the trunk from a sensor that is progressively cooled as the sap flow in the xylem increases (David et al. 2002). For such, a previous calibration was necessary. The sap flow model was adjusted for the African mahogany from the monitoring of three plants grown in constant water table lysimeters, as described in Sérvulo et al. (2017), resulting in the following equation:

$$F = 268.25 \cdot 10^{-6} \times k^{1.231} \times A_S \tag{4}$$

where F is the sap flow ($m^3\ s^{-1}$), k is the flow density ($m^3\ s^{-1}\ m^{-2}$), and A_S is the active xylem area (m^2) estimated from visual and anatomical analysis of wood, which allowed to observe the transition of the initial wood to the latewood in segments by observing the following relation:

$$A_S = 0.65836 \times A_T \tag{5}$$

where A_S is the area of sapwood (m^2) and A_T is the section total area.

The sap flow ($m^3\ s^{-1}$) was measured for 1 year from October/2014 to October/2015 (Fig. 1). Data was obtained using a CR-1000 (Campbell Scientific LTDA) associated with AM 1632 Relay Multiplexer. Readings were taken at 30-s intervals and the means stored every 15 min. Sensors were built with hypodermic needles 2.0 mm in diameter and 10.0 mm in length, externally coiled with constantan, containing a type T thermocouple (copper-constantan) inside. The upstream sensor resistance was constantly powered with 0.1 W and regulated by a power supply. The temperature difference was obtained by the connection of copper-constantan thermocouples.

A heat dissipation probe (HDP) was installed on the trunk of each tree at 0.20 m minimum distance from ground to reduce interference from direct radiation. Sensors were vertically spaced at 0.10 m (Clearwater et al. 1999). For this, the trunk of each tree was drilled using a drill (3.0 mm drill) in the defined positions to depth of 1.0 mm plus the thickness of the bark. Then, a carbon steel tube (3.0 mm in diameter and

1.0 mm in length) was inserted. Sensors were wrapped with thermal paste and positioned inside the respective tubes. Afterwards, the stem segment was wrapped with aluminum foil by forming "skirt" insulation (Vellame et al. 2011). A strip of aluminum foil enveloped the stem in the lower portion of the HDP, minimizing the effect of radiation and wind currents on the readings. Natural thermal gradients (NTG) were determined by using an unheated HDP inserted in a reference tree. NTG readings occurred at 30-s intervals and means were stored every 15 min.

Daily transpiration (T) was obtained by integrating the hourly sap flow. Variations in daily average vapor pressure deficit (DVP_d) and incident global solar irradiation (Rs) were used to evaluate the course of transpiratory flow on an hourly scale. The transpiratory flow is better evaluated when comparing trees of the same leaf area, because the process occurs on its surface and, proportionally, depending on its extension. Bearing in mind this biometric characteristic is not constant among monitored individuals, leaf area was used as scale parameter to facilitate comparisons between treatments (T_{LA} = L day^{-1} m^{-2} leaf area). In this case, standardizing transpiration by leaf area allowed the comparison between individuals of different sizes on the same representative scale. This standardization has been successfully applied in studies on tropical species (Meinzer et al. 1997), North American natives (Ewers et al. 2002), acidic lime (Marin et al. 2002), coffee (Marin 2003), Indian neem (Seixas 2009) among others.

Statistical analyses

Biometric variables were compared by the Student's t test at 5% of error probability between the treatments initially irrigated and non-irrigated. Furthermore, regression equations were adjusted to different times and biometric variables. The same analyses were made for the variable plant transpiration.

The relationships between transpiration by leaf area (T_{LA}), meteorological variables (DVP_d, T_a, ET_0, and Rs) and soil water storage were evaluated by means of linear regression, by the coefficient of determination (R^2) and Pearson's correlation coefficient (r).

Partial water-use efficiency (WUEp, dm^3 m^{-3} H_2O) was used to compare the increase in trunk volume between treatments, calculated for the period from February to August 2015 (Eq. [6]):

$$WUEp = \frac{IV_{TR}}{T} \tag{6}$$

where IV_{TR} is the increase in trunk volume (dm^3) and T is the transpiration (m^3 H_2O) accumulated in the period.

Results

Agrometeorological aspects and variation in soil water storage

The air temperature (T_a) during 13 months of evaluation varied between 16.7 and 29.2 °C, mean of 22.4 °C (Fig. 2), and annual mean thermal amplitude of 12.4 °C. The lowest amplitude values were observed in December/2014 (8.9 °C) and February/2015 (4.6 °C).

The highest amplitude values occurred in August 2014 (20.0 °C) and 2015 (16.2 °C). The mean relative air humidity was 72.1%, minimum value in August (52.6%) and maximum value in April (85.9%) (Fig. 2).

The maximum daily Rs value was recorded between 12:00 and 13:00 on days without rain. The monthly average for the monitoring interval of the African mahogany ranged from 154.6 W m^{-2} (March/2015) to 292.3 W m^{-2} (January/2015) (Fig. 2). The photoperiod (N, hours) showed maximum value in December (13 h) and minimum value in June (11 h) (Fig. 2).

Daily U_2 ranged from 0.24 m s^{-1} (March/2015) to 0.83 m s^{-1} (June/2015). There was difference between diurnal and nocturnal wind speeds, increasing during the day, decreasing in the afternoon and evening. In the daytime, the minimum speed was 0.41 m s^{-1} and the maximum speed was 1.50 m s^{-1}. The highest values of mean wind speed coincide with the dry season of the region, while the lowest values occurred in the rainy season (Fig. 2d). The east-southeast (ESE-21.5%) and eastern (E-19.7%) winds predominated in the dry period with predominance of the southeast winds (SE-12.7%) during the rainy season.

The average annual accumulations of ET_0 and rain were 1636 mm and 1100 mm from March/2014 to October/2015. The climatological normal was around 1400 mm year^{-1}. December/2014 (22.6 mm) and January/2015 (53.9 mm) had rainfall below the monthly climatological normal (January = 227 mm; = 237 mm) (Fig. 3).

Due to the fact that precipitation has been ≈ 85% lower on average, there was lower water storage potential in the soil causing a marked water deficit in the dry season of 2014 and implying lower water storage in the rainy period of 2015 (Fig. 3).

Plant growth

According to the biometric assessment, the initially irrigated treatment (IT) showed higher averages for all variables in all periods of assessment, except for plant height at first evaluation and for trunk volume when compared to non-irrigated treatment (NIT) (Table 1).

The linear regression analysis (F of significance < 0,05) showed marked increase in the IT, with larger angular coefficients compared to NIT, except for the trunk volume (TRV),

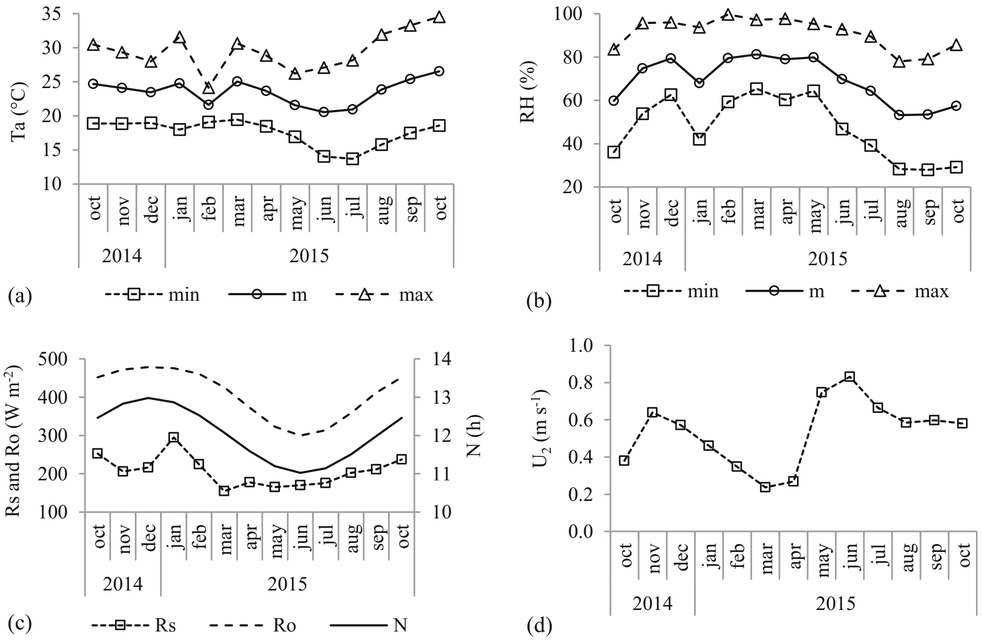

Fig. 2 Air temperature T_a (**a**), relative humidity of air *RH* (**b**), incoming global solar radiation (*Rs*), extraterrestrial solar radiation (*Ro*), photoperiod (*N*) (**c**), and wind speed (U_2) registered in the experimental area Bonfinópolis, GO, Brazil, from October/2014 to October/2015

which presented approximate coefficients (Fig. 4). In addition, there was significant difference in growth rates only in the last assessment, and for LDM, DBH, and LA, with higher averages in the irrigated treatment (Fig. 4).

The NIT treatment had 24.1% lower leaf area than the IT during the evaluation period, as well as lower growth rates (Fig. 4).

Significant and positive correlations ($r > 0.80$) were found only among variables expressing growth rate and mean solar irradiation of the period between evaluations. Also, the accumulated water deficit in August (*AWD* = 48.4 mm) was not enough to limit the growth of 3-year-old plants. This may have occurred due to *AWD* overestimation through high available water capacity (*AWC*) of 300 mm (Fig. 3).

The evolution in trunk volume growth (TRV, m^3) combined to the absolute water consumption (mm), similar in both treatments at the interval between February and August 2015, corresponded to the water use efficiency of approximately 2.33 dm^{-3} m^{-3} H_2O (trunk volume produced per volume of transpired water).

Transpiration by sap flow measurements

African mahogany plants transpired on average 18.8 L m^{-2} in the treatment initially irrigated during the rainy season and 11.3 L m^{-2} in the dry period. Non-irrigated treatment obtained values significantly different only to rainy season (14.3 L m^{-2}) (Table 2). Initially, irrigated plants had higher transpiration

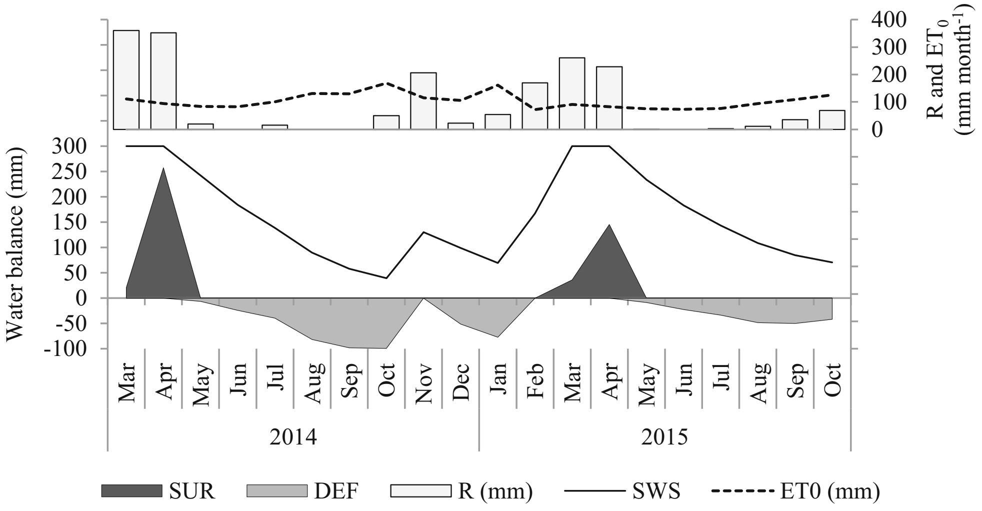

Fig. 3 Monthly sequential water balance (Thornthwaite and Matter 1955) from March/2014 to October/2015 period, for Bonfinópolis, GO, Brazil Water surplus (SUR), water deficit (DEF), rainfall (R), soil water storage (SWS), potential evapotranspiration (ET_0). Available water capacity AWC = 300 mm

Table 1 Biometric variables of African mahogany: height (H, m), leaf dry matter (LDM, kg), trunk volume (TRV, m^3), breast height diameter (BHD, m), and leaf area (LA, m^2), for initially irrigated (IT) and non-irrigated (NIT) plants

Times	IT H	NIT H	IT LDM	NIT LDM	IT TRV	NIT TRV	IT BHD	NIT BHD	IT LA	NIT LA
1	6.6A[a]	5.8A	5.0A	3.8B	0.04A	0.03A	0.11A	0.07B	42.3A	23.1B
2	7.7A	6.0B	6.1A	4.4B	0.05A	0.04A	0.12A	0.08B	50.1A	25.8B
3	8.6A	7.1B	6.8A	4.2B	0.06A	0.05A	0.13A	0.07B	57.3A	26.4B
4	10.1A	8.1B	7.9A	4.6B	0.07A	0.06A	0.14A	0.09B	64.8A	34.1B
$\overline{X}$	8.24	6.75	6.45	4.25	0.05	0.05	0.12	0.08	53.6	27.3
CV%	14,7		11,2		26,5		9,1		15,2	

[a] Means followed by the same capital letter in the row do not differ statistically from each other by the Student's *t* test at the 5% probability level of error. $\overline{X}$: mean value. CV%: coefficient of variation

Bonfinópolis, GO, Brazil, 2014–15

under water availability conditions, as well as in the mean of the period, and transpired 1.6 L m^{-2} more than non-irrigated plants (Table 2).

Regression equations were adjusted to the irrigated and non-irrigated treatments as a function of time, in which a transpiration increase trend during rainy periods was observed. However, the plants that were not previously irrigated had lower values of transpiration even in the periods without water deficit (Fig. 5).

Plants initially irrigated transpired 24% of ET_0 and non-irrigated plants transpired 16% of ET_0 for the entire evaluation period (Fig. 3; Table 2).

From March/2015, non-irrigated plants showed gradual increase in transpiration and exceeded plants initially irrigated in July and August/2015 (Table 2). Water deficit was 33.6 mm and 48.4 mm in these months and the high evaporative demand was corroborated by the relative evapotranspiration ETR/ETc value between 0.49 and 0.56

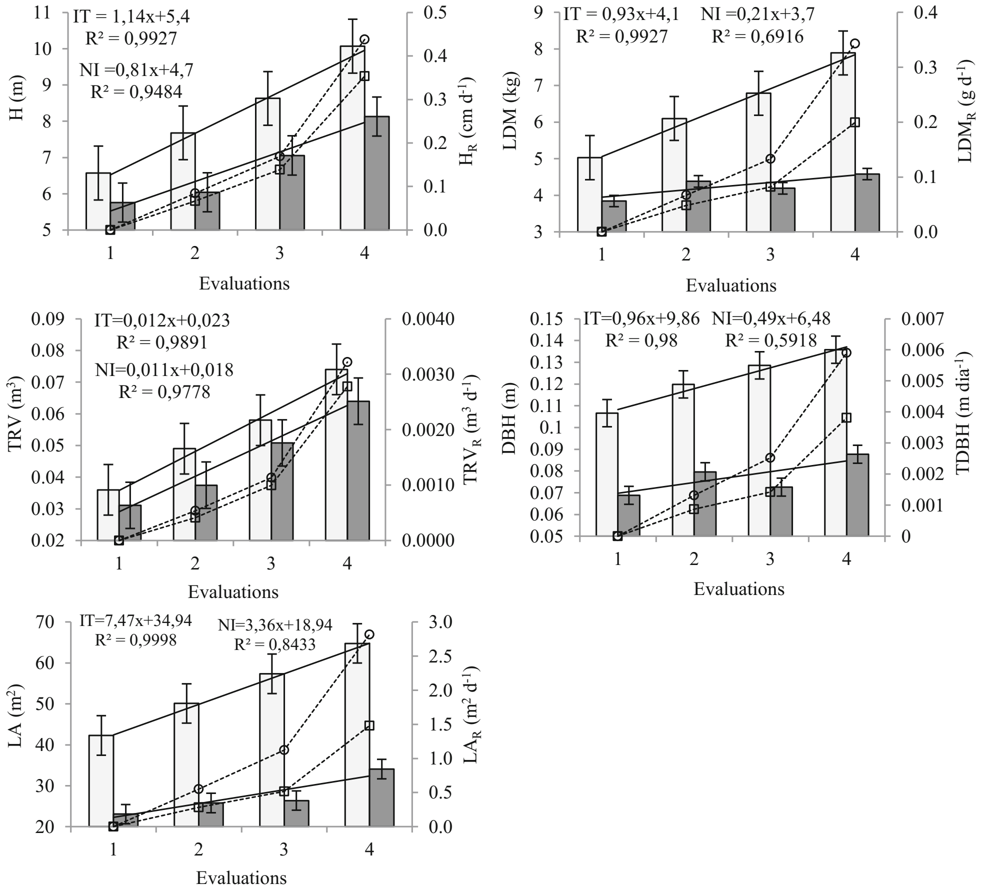

Fig. 4 Height of plants (H, m), leaf dry matter (LDM, kg), trunk volume (TRV, m^3), breast height diameter (BHD, m), and leaf area (LA, m^2), to African mahogany cultivated with initially irrigated (IT: light gray columns) and not irrigated (NI: dark gray columns), as well as their respective growth rates (H_R, LDM_R, TRV_R, BHD_R, LA_R), for irrigated cultivation (○) and not irrigated (□). The error bars correspond to the standard deviation. Bonfinópolis, GO, Brazil, 2014–15

Table 2 Monthly transpiration of African mahogany, per unit of leaf area (L m^{-2}), and their respective standard deviations (σ) and coefficient of variation (CV%), cultivated from 2.5 years of age Bonfinópolis, GO, Brazil, 2014–15

Year	Month	Initially irrigated		Not irrigated		CV%
		L m^{-2a}	σ	L m^{-2a}	σ	
2014	Oct	33.0 A	9.5	15.4 B	5.4	12.2
	Nov	24.3 A	7.1	18.2 B	9.8	11.8
	Dec	19.4 A	5.4	14.0 B	9.2	11.6
2015	Jan	–	–	–	–	
	Feb	13.3 A	4.1	12.5 A	6.6	9.7
	Mar	12.5 A	3.5	13.7 A	5.1	9.6
	Apr	10.2 A	5.4	11.8 A	4.3	8.9
	May	–	–	–	–	
	Jun	–	–	–	–	
	Jul	11.0 B	1.9	20.5 A	6.7	12.4
	Aug	9.7 B	1.2	16.8 A	2.3	11.3
	Sep	12.8 A	4.2	10.5 A	5.2	11.5
	Oct	11.7 A	2.5	8.6 A	1.8	11.8
Rainy	Oct-Apr	18.8 A	5,8	14.3 B	8,0	10,6
Dry	May-Oct	11.3 A	2,5	14.1 A	10,1	11,7
Mean	Period	15.8 A	4,5	14.2 A	8,9	11,1

[a] Means followed by the same upper case letter in the row do not differ significantly from each other by the Student's *t* test ($\alpha = 5\%$)

(based on Fig. 3). In this period, the transpiration of irrigated plants was inversely proportional to the diurnal vapor pressure deficit, responding discreetly to the solar radiation stimulus and no significant relationship with potential evapotranspiration and mean air temperature (Tables 3 and 4). The non-irrigated treatment maintained transpiration and was independent of the agrometeorological variables in this period (Tables 3 and 4).

The transpiration of non-irrigated plants in July and August/2015 was equivalent to that observed between October and December 2014 with a cumulative maximum water deficit of 124.7 mm (6 months previously). In contrast, initially irrigated plants had difficulties in recovering the transpiratory rate during the deficit period, as observed in the negative response of transpiration to VPD_d. There was recovery only in September after rainfall (35 mm). Similar hydraulic properties in treatments were verified by the similarity in the ratio LA/A_S (leaf area/sap conduction area), constant over time and equal to 1.50 m^2 cm^{-2}. This eliminates the possibility of modification in internal resistance to water movement.

The larger leaf area in IT (Fig. 4) promoted higher transpiratory flow and consequent advance of the water deficit condition due to soil water depletion (Fig. 3). Considering the months when there was no difference in transpiration between treatments (Oct, Nov, and Dec/2014; Feb, Mar, Apr, Sep, and Oct/2015), transpiration varied by on average 0.90–1.38 L m^{-2} day^{-1}.

Using the crop spacing, African mahogany transpired on average 0.27–1.07 mm day^{-1}. The increase in stomatal resistance due to increased VPD_d was probably insufficient to reduce transpiration (Tables 3 and 4), which indicates non-limiting water conditions in soil. In months where there were no differences, trees responded more to the VPD_d and the Rs, while the direct response to ET_0 occurred in months with ETR/ETc ratio below 1.0. The mean and maximum air temperatures also had positive effects on the process during this period (Tables 3 and 4).

Also, the nebulosity may explain limited transpiration in periods of greater water availability in soil, especially on rainy days (February to April). However, wind speed had no direct effect on the transpiration process in the daily scale, but it influenced positively in some periods (Fig. 2).

In general, forest development under irrigation in the initial 2 years and with no irrigation from the second year was not enough to guarantee better productivity to the African mahogany. However, larger leaf area and diameter at breast height were observed in the irrigated treatment

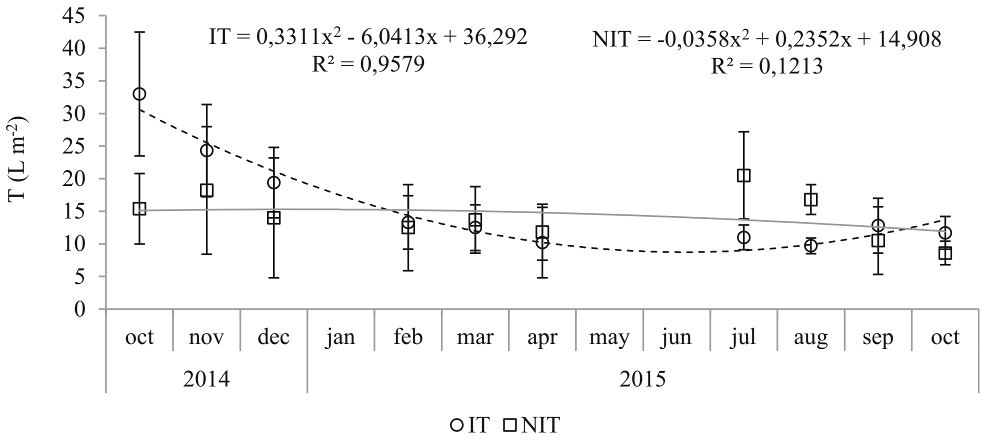

Fig. 5 Monthly transpiration of African mahogany, per unit of leaf area (T, L m^{-2}), and their respective standard deviations (error bar), for irrigated cultivation (IT, ○) and not irrigated (NIT, ◻). Adjustment of regression equations in function of time to irrigated (dotted line) and not irrigated (line). Bonfinópolis, GO, Brazil, 2014–15

Table 3 Correlation analysis between African mahogany transpiration (L m^{-2}) and diurnal vapor pressure deficit (DVP_d, kPa) and with mean air temperature (T_a, °C)

Year	Month	DVP_d				T_a			
		Mean	*p* value	R^2	Pearson	Mean	*p* value	R^2	Pearson
2014	Oct	2.1	6.8E-07*	0.65	0.81	24.9	1.5E-03*	0.35	0.59
	Nov	0.9	2.5E-04*	0.41	0.57	23.0	1.9E-02*	0.19	0.36
	Dec	0.8	1.7E-06*	0.64	0.80	22.5	2.4E-07*	0.69	0.83
2015	Jan	–	–	–	–	–	–	–	–
	Feb	0.9	8.7E-01^{ns}	0.00	0.01	23.0	2.7E-01^{ns}	0.07	0.22
	Mar	0.6	3.1E-03*	0.39	0.53	23.1	1.3E-01^{ns}	0.12	0.23
	Apr	0.8	2.9E-01*	0.14	0.37	22.5	6.3E-01^{ns}	0.03	0.17
	May	–	–	–	–	–	–	–	–
	Jun	–	–	–	–	–	–	–	–
	Jul	1.5	–	–	–	19.8	–	–	–
	I	–	8.1E-03*	0.52	−0.72	–	8.5E-01^{ns}	0.00	−0.06
	NI	–	8.1E-01^{ns}	0.01	−0.08	–	3.6E-01^{ns}	0.09	−0.29
	Aug	2.2	–	–	–	21.7	–	–	–
	I	–	5.3E-01^{ns}	0.02	0.04	–	7.7E-02^{ns}	0.18	−0.39
	NI	–	2.2E-01^{ns}	0.61	−0.78	–	1.9E-01^{ns}	0.66	−0.81
	Sep	2.4	1.4E-05*	0.64	0.79	24.8	1.7E-03*	0.41	0.44
	Oct	2.4	7.4E-01^{ns}	0.01	−0.11	25.9	5.6E-01^{ns}	0.03	−0.18

*Significant at 5% of probability of error; ^{ns} not significant

and eventual higher transpiration in the non-irrigated treatment (L m^{-2}). Also, different responses of transpiration in treatments to the medium stimuli (soil water storage and climatic conditions) are better explained by the influence of the leaf area in the transpiratory process than by both water regimes.

Table 4 Correlation analysis between African mahogany transpiration (L m^{-2}) and reference evapotranspiration (ET_0, mm), and the global solar radiation (*Rs*, W m^{-2} dia^{-1})

Ano	Mês	ET_0				*Rs*			
		Mean	*p* value	R^2	Pearson	Mean	*p* value	R^2	Pearson
2014	Oct	5.4	5.6E-04*	0.40	0.63	258.0	3.9E-04*	0.70	0.72
	Nov	3.8	3.9E-01^{ns}	0.03	0.12	206.0	5.0E-02*	0.77	0.88
	Dec	3.4	1.2E-07*	0.71	0.84	216.6	3.4E-05*	0.80	0.90
2015	Jan	–	–	–	–	–	–	–	–
	Feb	2.8	1.3E-01^{ns}	0.12	0.32	–	–	–	–
	Mar	3.0	1.1E-01^{ns}	0.14	0.26	154.6	3.8E-03*	0.90	0.66
	Apr	2.8	9.8E-01^{ns}	0.00	−0.01	177.7	3.8E-01^{ns}	0.19	−0.44
	May	–	–	–	–	–	–	–	–
	Jun	–	–	–	–	–	–	–	–
	Jul	2.5	–	–	–	294.8	–	–	–
	I	–	7.0E-01^{ns}	0.02	−0.13	–	6.3E-01^{ns}	0.02	−0.16
	NI	–	5.9E-01^{ns}	0.03	−0.17	–	7.1E-01^{ns}	0.01	0.12
	Aug	3.0				202.3			
	I	–	5.7E-01^{ns}	0.02	0.17	–	3.7E-04*	0.85	0.86
	NI	–	8.1E-01^{ns}	0.04	0.19	–	–	–	–
	Sep	3.6	2.0E-07*	0.77	0.91	211.2	4.2E-06*	0.68	0.88
	Oct	4.0	4.8E-01^{ns}	005	−0.22	259.5	2.3E-01^{ns}	0.13	−0.36

*Significant at 5% of probability of error; ^{ns} not significant

Discussion

Edaphoclimatic conditions

African mahogany originates from the West African Coast-AW/AS climate (Köppen and Geiger 1928). In Brazil, suitable edaphoclimatic conditions were detected in 55.62% of the national territory. As for the climate, regions of average air temperature between 23 and 29 °C and rainfall between 830 and 3000 mm year^{-1} were considered suitable. The types of suitable soils were Argosol, Oxisol, Neosol, Quartzonic, Litolic, Insular, and Equatorial (Casaroli et al. 2018). These values corroborate the average climatic data found in this study, as well as the type of soil used in the experiment.

It is worth mentioning that although annual rainfall is classified as suitable, these are not homogeneously distributed throughout the year, which highlights the water deficit as a limiting factor for African mahogany growth in the Cerrado of Goiás (Alves Júnior et al. 2017; Alves Júnior et al. 2016; Casaroli et al. 2017; Casaroli et al. 2016).

Biometric measurements and water stress

Some plant protection mechanisms are activated in response to adverse environmental conditions to growth. The osmotic regulation, one of the physiological mechanisms for maintenance of cellular turgescence, stands out under conditions of low soil water potential (Marijuan and Bosch 2013). This mechanism confers protection for short periods of stress and it is important when conditions soon normalize. According to Flexas and Medrano (2002), plants submitted to water deficit may have lower plant growth due to stomatal limitation to CO_2 influx, photosynthetic apparatus photochemical damage, reduced ATP synthesis, decreased Rubisco (ribulose-1,5-bisphosphate carboxylase oxygenase) activity, or decreased regeneration rate.

The osmotic regulation is established by the accumulation of some compatible solutes in the vacuole or cytosol, such as proline, glycine betaine, trehalose, sucrose, polyamines, mannitol, pinitol, among others. These solutes contribute to the water balance maintenance and the preservation of integrity of proteins, enzymes, and cell membranes (Ashraf et al. 2011). They also have osmoprotective function against toxic byproducts of metabolism resulting from water stress. The amino acid proline is the most studied compatible solute because of its responsiveness to stress conditions (Verbruggen and Hermans 2008).

Young plants of African mahogany (315 days) are tolerant to water deficit because they have high stomatal sensitivity to water deficit and significant accumulation of proline in leaves. Proline decreases leaf water potential by increasing water absorption capacity of plants and attenuating the effects of water deficit on the plant's relative water content (Albuquerque et al. 2013). In plants of Brazilian mahogany (*Swietenia macrophylla* King) under stress, proline content can increase up to 400%, minimizing the drought effect (Cordeiro et al. 2009). Both young plants of Brazilian mahogany, *Swietenia macrophylla* (Cordeiro et al. 2009) and Andiroba plants, *Carapa guianensis* (Gonçalves et al. 2009), satisfactorily tolerate periods of 15 to 30 days of water deficit from this mechanism.

Although African mahogany plants have certain tolerance to water deficit (Albuquerque et al. 2013; Zhao et al. 2015), they have their growth increased when irrigated (Alves Júnior et al. 2017; Casaroli et al. 2017). This behavior was detected in this study, through the highest growth of height, leaf dry matter, breast height diameter, and leaf area, in the irrigated treatment. In the literature, irrigated trees show significant increase of dry biomass in the shoots (Gentil 2010; Fernandes et al. 2012).

It is worth mentioning that plant growth and development result of three levels of control: intracellular (genetic control), intercellular (involves regulatory substances), and extracellular (environmental conditions, involving physical and biological factors). Thus, the heterogeneity in biometric characteristics corroborated by coefficients of variation between 20 and 40% is also attributed to the possible genetic variation, since seedlings used in planting were seminal (Taiz and Zeiger 2009). Silva (2010) highlights the irregular production and the formation of heterogeneous populations as the main disadvantages of using seedlings. Trees of *Khaya ivorensis* reproduce sexually, probably via allogamy, which allows high diversity within populations (heterozigosity = 0.56) (Soares 2014), but lower than other wild plants such as *Pinus taeda* 0.45 (Mercer 2011) and *Tectona grandis* 0.35 (Alcântara 2009).

In the forest studied (120 days after planting), the non-irrigated plants had 97% smaller LA than the irrigated ones, reaching 81.4% after the rainy season (540 days after planting) (Casaroli et al. 2017). This effect can still be seen in the growth and development of the African Mahogany leaf area at 1249 days after planting.

In the same area of the experiment, Alves Júnior et al. (2017) observed that differences in diameter of breast height (DBH) between irrigated and non-irrigated plants showed reduction trend of 19.6% (680 days) to 14.9% (1249 days). Irrigation clearly contributes to changes in plant's hydraulic architecture and reflects in greater diameter growth and formation of less thick cell walls (Nichols and Waring 1977).

The DBH growth was similar to that of Andiroba (*Carapa guianensis*). In this case, reduced water supply in the dry season of the Central Amazon region was compensated by the increased irradiance, providing the same DBH growth rate throughout the year (Camargo and Marenco 2012). The difference in the pluviometric regimes of the region in this study and in the region observed by Camargo and Marenco (2012) indicates that individuals of *Khaya ivorensis* can have access to water even in the dry season. This conditions them to continue growth without damage and/or to develop mechanisms of resistance to the water deficit.

The fact that monthly water deficit blades were not enough to limit plant growth can be explained by the deficit overestimation due to the use of available water capacity ($AWC = 300$ mm). Thus, considering the average AWC for Cerrado soils around 130 mm/m (Freitas Júnior and Silva 1984), the effective depth of root system (Ze) of African mahogany plants should be maximum 2.30 m, which may be underestimated. For example, the adult Indian Nim (Meliaceae) root system may have depth Z = 15 m (Neves et al. 2003) while other perennial tropical forest species have Z = 6.5 m as a global average (Canadell et al. 1996) and Z = 18 m as Brazilian average (Nepstad et al. 1994).

Irrigated plants (24% ET_0) showed higher transpiration than non-irrigated ones (16% ET_0) for the entire evaluation period. For black acacia (R. *pseudoacacia*), percentages vary between 10 and 16% (Zhang et al. 2015).

The water use efficiency given by volume of trunk produced by volume of transpired water was similar to that observed in *Acacia mangium* (2.3 dm^{-3} m^{-3} H_2O) and lower than that of *Eucalyptus grandis* (4.3 dm^{-3} m^{-3} H2O), both aged between 2.8 and 3.8 years (Deus Junior 2014). This proves greater tolerance of African mahogany to regions with less water availability.

Plant transpiration

Some authors report seasonal and interannual variations in transpiration at different time scales. On a monthly scale, daily transpiration is more strongly correlated with daily solar irradiation and mean diurnal vapor pressure deficit (VPD). Monthly variations of transpiration are mainly correlated to leaf area indexes and VPD_d. On annual scale, the positive relationship between transpiration and soil moisture conditions was highlighted. Rainfall does not show strong correlation with transpiration at any seasonal or annual scale (Zhang et al. 2015).

Similar hydraulic properties of treatments were verified by the similarity in LA/A_S (leaf area/sap conduction area) ratio, constant over time and equal to 1.50 m^2 cm^{-2}, which discards the possibility of modification in the internal resistance to water movement. This LA/A_S ratio describes the relative capacity of water transport in relation to the transpiration demand (Meinzer et al. 1997).

Under water deficit conditions, plants perform stomatal closure as a way to avoid excessive water loss and turgescence (Albuquerque et al. 2013). Costa et al. (2015) observed 92% reduction in transpiration of young plants of aroeira (*Myracrodruon urundeuva*) as a consequence of the stomatal regulation under a marked water deficit condition.

In this study, irrigated and non-irrigated treatments had no significant difference in the average transpiration in some occasions and mainly in the rainy season. We infer that irrigated plants are more sensitive than non-irrigated ones, since transpired volume tends to decrease significantly under water deficit conditions. Other cultivated tree species show greater variation between irrigated and non-irrigated plants when compared to our study, such as mango (0.36 to 3.00 L m^{-2} day^{-1}, respectively) (Oliveira et al. 2009) and papaya (0.26 to 3.06 L m^{-2} day^{-1}, respectively) (Coelho Filho et al. 2003). On the other hand, other species showed lower variation, such as Tahiti acid lime (0.4 and 1.1 L m^{-2} day^{-1}, respectively) (Delgado-Rojas 2003) and apple tree (0.78 and 1.78 L m^{-2} day^{-1}, respectively) (Pereira et al. 2011).

Another way of evaluating the transpiration of African mahogany plants is to use the crop spacing by transforming L m^{-2} into mm. Thus, plants transpired 0.27–1.07 mm day^{-1}, interval close to that of other woody species such as *M. polymorpha* 0.17–1.17 mm day^{-1} (Santiago et al. 2000), *Acer Sacharum* Marsh 0.6 mm day^{-1} and *Abies balsamea* 0.9 mm day^{-1} (Ewers et al. 2002), *Pinus silvestris* 0.69–2.62 mm day^{-1} (Tang et al. 2015). However, African mahogany transpiration was lower than that observed in Indian Nim (0.5–4.5 L m^{-2} leaf) cultivated under soil moisture condition in field capacity (Seixas 2009) and in non-irrigated eucalypt (4.4–8.7 mm day^{-1}) (Gentil 2010).

In studies on several other woody species, transpiration of individuals was limited by the vapor pressure deficit and the water available through the stomatal regulation (Ewers et al. 2002; David et al. 2002; Vellame 2010; Zhang et al. 2015). This is explained by the need to maintain the plant water status and adequacy to the water flow in the soil (Pataki et al. 2000).

The vapor pressure deficit directly affects daily transpiration because the difference between the vapor pressure in the stomatal chamber and the air adjacent to the leaf is the determining factor for water loss in form of vapor to the environment. Zhang et al. (2015) found VPD_d and Rs directly affecting transpiration of forest species on a daily and monthly scale. However, the influence of these climatic factors becomes limited when analyzed on a seasonal scale, being governed by phenological and environmental factors. In studies on citrus (Hall et al. 1975; Meyer and Green 1981) and macadamia (Lloyd 1991), the increase in diurnal vapor pressure deficit was not enough to reduce transpiration. For Zhang et al. (2015), the relationship of transpiration with soil water content is more easily observed on a year-on-year basis, mainly due to the recharge through precipitation during the previous years be responsible for the current soil water condition.

There was limited transpiration, especially in the rainy season, which can be explained by the nebulosity and lower incidence of solar radiation. Salati (1987) states that nebulosity leads to lower accumulated irradiance in the day and this may limit photosynthesis and simultaneous processes in leaves that are usually exposed directly to solar radiation.

Although the wind speed did not have direct effect on the transpiration process on the daily scale, it showed positive trends in some periods. According to the Beaufort scale, diurnal winds were classified as "calm" and "light breeze" with values between 0.0 and 2.9 m s^{-1}. The wind action directly interferes with transpiration rate by removing water vapor near the leaves (Pereira et al. 2011), but its excess increases proportionally to transpiration to the point of inducing stomatal closure (Ataíde et al. 2015).

Conclusions

Planting of African mahogany non-irrigated promotes greater canopy heterogeneity and lower growth indicators. Although both the height and the volume of timber produced under irrigated and non-irrigated conditions up to 2 years of age, evaluated between 2.5 and 3.5 years of age, are not significantly affected by the absence of irrigation, there is a positive effect of irrigation on plant growth.

African mahogany transpiration responds to global solar radiation stimuli, diurnal vapor pressure deficit, evapotranspiration, and mean air temperature.

Considering the months in which there was no difference in the transpiration between the treatments in the field (Oct, Nov, and Dec/2014; Feb, Mar, Apr, Sep, and Oct/2015), transpiration varied on average 0.9–1.38 L m^{-2} leaf day^{-1} or 0.27–1.07 mm day^{-1}.

African mahogany grown without irrigation consumes less water in its physiological processes (in absolute values) due to the smaller leaf area. However, transpiration per unit of leaf area was proportional most of the time in both systems evaluated.

Irrigation of African mahogany plants in the first 2 years of age maintains higher growth after its break off for at least two subsequent years. However, non-irrigated plants are similar in terms of trunk volume and transpiration rates, especially in the dry season of the year.

On the other hand, studies are needed to prove the economic viability of applying irrigation to African mahogany crops in the long term.

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