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African Mahogany transpiration with Granier method and water table lysimeter

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sap flux
transpiration
lysimeter
sapwood

ABSTRACT
The thermal dissipation probe (Granier method) is useful in the water deficit monitoring and irrigation management of African Mahogany, but its model needs proper adjustment. This paper aimed to adjust and validate the Granier sap flux model to estimate African Mahogany transpiration, measure transpiration using lysimeter and relate it to atmospheric water demand. Weather conditions, transpiration and sap flux were monitored in three units of 2.5-year-old African Mahogany trees in constant water table lysimeter, in Goiânia, GO. Sapwood area (SA), leaf area (LA), transpiration measured by lysimeter (T_{LYS}) and estimated by sap flux (T_{SF}) were evaluated. The SA comprised 55.24% of the trunk's transversal section. The LA varied from 11.95 to 10.66 m^2. T_{LYS} and T_{SF} varied from 2.94 to 29.31 and from 0.94 to 15.45 L d^{-1}, respectively. The original model underestimated transpiration by 44.4%, being the adjusted equation $F = 268.25 \cdot k^{1.231}$. SA was significant ($F < 0.05$). Due the root confinement, the transpiration showed low correlation, but positive, with the atmospheric water demand.

Palavras-chave:
Khaya ivorensis
fluxo de seiva
transpiração
lisimetria
área do xilema

Transpiração de Mogno Africano com método de Granier e com lisímetro de lençol freático constante

RESUMO
No monitoramento do déficit hídrico e no manejo da irrigação do Mogno Africano, o uso da sonda de dissipação térmica (método de Granier) é útil porém necessita de ajuste do modelo. Objetivou-se ajustar e validar a equação proposta por Granier para estimativa da transpiração em Mogno Africano e a partir da lisimetria medir a transpiração e relacioná-la com a demanda hídrica atmosférica. Monitoraram-se as condições meteorológicas, a transpiração e o fluxo de seiva em três plantas de 2,5 anos de idade de Mogno Africano em lisímetros de lençol freático constante, em Goiânia, GO. Avaliou-se: a área de xilema ativo (AS), a área foliar (AF), a transpiração medida pelo método do lisímetro (T_{LIS}) e estimada pelo fluxo de seiva (T_{FS}). A AS compreendeu 55,24% da área da seção transversal do caule. A AF variou entre 11,95 e 10,66 m^2. T_{LIS} e T_{FS} variaram de 2,94-29,31 e 0,94-15,45 L d^{-1}, respectivamente. O modelo original subestima a transpiração em 44,4% sendo o modelo ajustado $F = 268{,}25 \cdot k^{1{,}231}$. AS foi significativo ($F < 0{,}05$). Devido ao confinamento radicular, a transpiração teve baixa correlação, porém positiva, com a demanda hídrica atmosférica.

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Introduction

The exploitation in non-traditional areas and the suspicion about the limitation of the yield of African Mahogany (*Khaya ivorensis*) under water deficit stimulate the search for information to quantify the water requirement of the species in the different development stages. In an initial stage, African Mahogany positively responds to irrigation and has physiological responses to the water deficit, indicating moderate tolerance (Albuquerque et al., 2013).

For the understanding about the water relationships of the crop, it is essential to know its physiological responses (stomatal opening, transpiration, accumulation of soluble carbohydrates, production of proline) to the stimuli from the surrounding environment (water in the soil, atmospheric evaporative demand).

Assuming the equivalence between the sap flux and transpiration flux of leaf surfaces, the sap flux measurement is used to estimate the transpiration of woody species, allowing to monitor their water functioning for a long period, under undisturbed natural conditions (Vellame et al., 2012).

The method developed by Granier (1987) estimates the transpiration from the thermal dissipation of a heated probe inserted in the stem, due to the sap flux. This behavior is related to the thermal and hydraulic properties of the wood of each species (Zhang et al., 1996).

The exponential model proposed by Granier is viable in the estimate of transpiration of woody species, provided that its equation is adjusted for each species (Vellame et al., 2009; 2012; Bush et al., 2010).

This study aimed to adjust the sap flux equation proposed by Granier to African Mahogany and relate its transpiration to leaf area and evapotranspiration.

Material and Methods

The experiment was conducted in Goiânia, GO, Brazil (16° 35' 53" S; 49° 16' 40" W; 735 m), whose climate is Aw, according to Köppen's classification, with well-defined dry and rainy seasons. The meteorological variables were measured by the automatic station EMCRX3000-GSM (Onset®), 240 m away from the experiment. Reference evapotranspiration was determined by the Penman-Monteith model (ET_{PM}, mm d^{-1}) (Allen et al., 2006). Evaluations occurred from October 11 to November 23, 2015, and from February 28 to May 10, 2015.

Three constant water table lysimeters (Figure 1) were used, installed at the field, filled with a layer of crushed stone (0.10 m) and sand (0.05 m), and the rest with dystrophic Red Latosol, with approximate density of 1,300 kg m^{-3}. Field capacity was determined by saturation and later drainage of the soil. Because the soil of the lysimeters was maintained at field capacity, its physical hydraulic attributes did not limit the conditions of water availability. Each lysimeter contained one 2.5-year-old African Mahogany plant and the soil was covered with a plastic canvas to eliminate water losses through evaporation and entry of rainwater. Transpiration measured by the lysimeter (T_{LYS}, L) was monitored every 24 h.

The lysimeter comprised a polyethylene water tank (500-L capacity) and the water was supplied by a set of reservoir and a level controller, connected to the lysimeter. The water table level was maintained until the soil layer of 1 cm, exceeding, from bottom to top, the layer of crushed stone and sand.

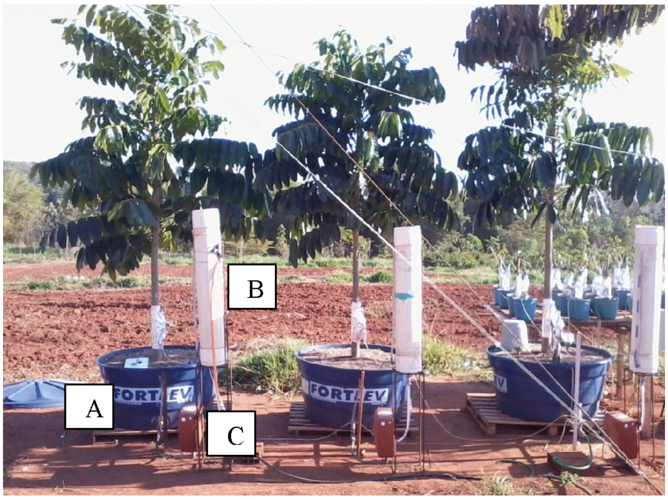

Figure 1. Constant water table lysimeters: PVC water tank (500-L capacity) (A), PVC water reservoir (pipe with diameter of 200 mm and height of 1.50 m) (B) and discharge box (C)

The sap flux was monitored using thermal dissipation probes (TDP) in intervals of 15 min and integrated for 24 h (transpiration - T_{SF}, L). The TDPs were composed of two 10-mm-long probes, connected to a data logger (CR21X and AM 16/32). One TDP was installed in the trunk of each tree at a minimum distance of 0.20 m from the soil and the probes separated by a vertical distance of 0.10 m (Clearwater et al., 1999).

The stem segment was involved with aluminum foils forming a "skirt" of thermal insulation (Vellame et al., 2011), besides a strip of aluminum foil involving the stem below the TDP. The natural thermal differences (NTD) were measured by an unheated TDP inserted in a reference tree.

The sap flux was estimated from readings of temperature differences by the TDP, following the Eq. 1, proposed by Granier (1987):

$$F = 118.99 \cdot k^{1.231} \cdot SA \quad (1)$$

where:
- F - sap flux, m^3 s^{-1};
- k - flux index, m s^{-1}; and,
- SA - sapwood area, m^2.

The flux index (k) was determined by Eq. 2:

$$k = \frac{(\Delta T_{max} - NTD) - (\Delta T - NTD)}{\Delta T - NTD} \quad (2)$$

where:
- k - flux index, m^3 s^{-1} m^{-2};
- ΔTmax - difference of temperature between the probes at null flux, °C;
- ΔT - instantaneous difference of temperature between the probes, °C; and,
- NTD - instantaneous natural thermal difference, °C.

Only the angular coefficient of the Granier model was adjusted (Taneda & Sperry, 2008; Vellame, et al., 2009; Bush et al., 2010). The equation was adjusted using the angular coefficient of the linear model with intercept equal to zero, obtained via regression analysis and fitted through the minimization of the absolute deviations between the means of five days of T_{SF} and T_{LYS}.

The T_{SF} was then related to the ET_{PM}, leaf area (LA - m²) and to the time of evaluation (TEv - days) through linear regression analysis. The parameters of the obtained models were subjected to the t-test and regression, by the F test.

The sapwood area (SA, m²) was estimated at the end of each evaluation period through the proportion in relation to the total area of the section. At the end of the experiment, the trees were cut and the transverse section discs of the base were removed (5.0-cm thick). The discs were photographed and the Image Pro Plus® image analysis software was used to determine the proportional area of bark, sapwood and heartwood (Vellame et al., 2011).

A hundred per cent of the leaves of a non-irrigated tree of same age of the monitored trees, from a commercial plantation close to the experiment, were removed to elaborate the leaf area estimation model, determined by Eq. 3, established by the relationship between the total leaf area and the product between the number, length and width of leaflets of the reference tree, with minimum sampling of 60% of the leaflets, obtained through regression analysis. Thus, the estimation error was equal to 3.59%, R² to 0.96 and Willmott's index of agreement (d) to 0.99.

$$LA = N_L \cdot \left(0.7161 \cdot W_m \cdot L_m\right) \quad (3)$$

where:

- LA - leaf area of the plant, m²;
- N_L - number of leaflets;
- W_m - mean width of leaflets, m; and,
- L_m - mean length of leaflets, m.

Results and Discussion

The values of T_{LYS} and T_{SF} varied from 2.94 to 29.31 L d^{-1} and from 0.94 to 15.45 L d^{-1}, respectively, which correspond to 0.28-2.45 and 0.09-1.29 L m^{-2} of leaf area. The ET_{PM} remained between 2.1 and 4.0 mm d^{-1} (Figure 2). The global radiation varied between 147.7 and 266.0 W m^{-2}, air temperature between 21.7 and 27.0 °C, and daytime vapor pressure deficit between 0.47 and 3.50 kPa.

T_{LYS} was 2.254 times higher than T_{SF}. Hence, it can be claimed that the original model of Granier underestimated the transpiration of African Mahogany by 44.4% (Figure 3).

In a reduced time scale (min or h), both the angular (α = 118.99) and potential (β = 1.231) coefficients of the Granier model can be adjusted. The daily monitoring scale of the present study allowed to adjust only the angular coefficient. Studies with various species point that only this latter adjustment is sufficient to correct the Granier equation and, in many cases, the adjustment of the potential coefficient is not significant (Taneda & Sperry, 2008; Bush et al., 2010).

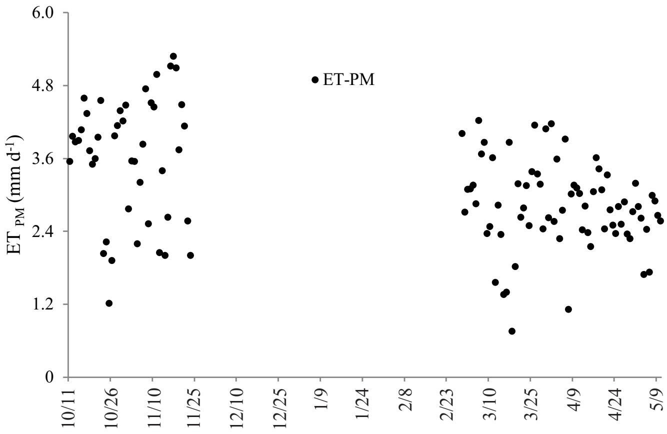

Figure 2. Daily values of evapotranspiration (period Oct/11-Nov/23/2014 and Feb/28-May/10/2015)

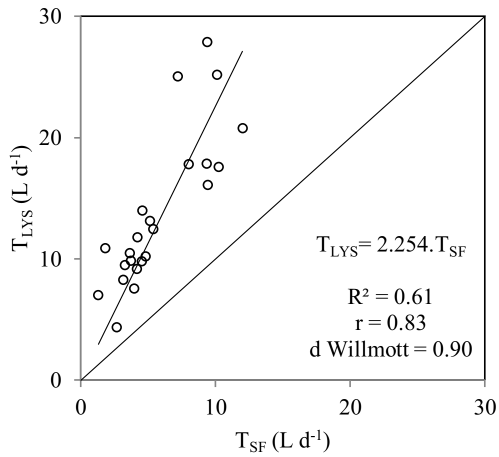

Figure 3. Relationship between means of five days of sap flux (T_{SF}) and actual transpiration (T_{LYS}) in African Mahogany, from the age of 2.5 years, in constant water table lysimeter (period Oct/11-Nov/23/2014 and Feb/28-May/10/2015)

The physical properties of the wood possibly have greater influence on the sensitivity of the Granier method compared with the flux density itself (Coelho et al., 2012), since the porosity of the material interferes with the factors of thermal dispersion, and the dispersion of heat does not depend much on the flow regime.

Based on that, the angular coefficient of the regression equation was adjusted, leading to Eq. 4:

$$F = 268.25 \cdot k^{1.231} \cdot SA \quad (4)$$

The T_{SF} before the adjustment of the Granier equation showed values from 40.0 to 76.2% lower compared with T_{LYS} (Figure 4). After the adjustment, T_{SF} showed values up to 46.2% lower and 36.3% higher compared with T_{LYS}. The greatest differences between T_{SF} and $T_{SF\ adjust}$ occurred in the months of October and November 2014, coinciding with higher daily transpirations (> 15 L d^{-1}) and higher evapotranspiration (Figure 2).

The maximum sap flux recorded on days of lower and higher transpiration varied between 0.29 and 3.66 L h^{-1}, considering the adjusted equation. The scale of daily evaluation prevented the verification of the occurrence of loss of sensitivity of the TDP, possibly responsible for the underestimation. Lundblad

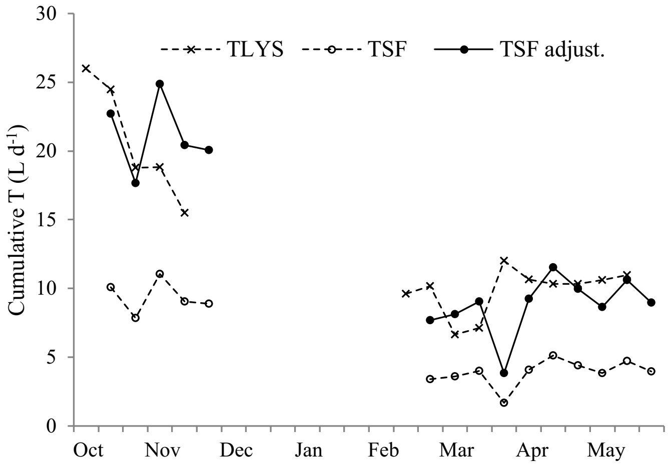

Figure 4. Mean transpiration (T) along five days of African Mahogany from the age of 2.5 years on, estimated by the sap flux equation of Granier (TSF), adjusted equation (TSF adjust.) and measured by lysimetry (TLYS) (period Oct/11-Nov/23/2014 and Feb/28-May/10/2015)

et al. (2001) observed, in Pine under maximum water transfer to the atmosphere (flux above 1.8 L h^{-1}), a 50% underestimation of transpiration by the TDP, while under water deficit and consequent lower transpiration flux the method correctly estimated transpiration. However, Vellame et al. (2009) report failure in the measurement of transpiration flux in "Tommy Atkins" mango with the adjusted Granier model, from 0.24 L h^{-1} on, underestimating transpiration by only 6.5%.

The digital image analysis of the discs pointed to percentages of bark (29.08%), sapwood (55.24%) and heartwood (15.68%). No nodes or heterogeneities were observed in the wood. The mean thickness of the bark was 1.94 cm. The mean thickness of the sapwood (7.03 cm) was used to obtain the total insertion of the probes in the SA. Consequently, the underestimation of the flux was not associated with the contact with the inactive xylem. In the adjustment of the Granier method for *Eucalyptus*, the flux index (k) was underestimated by 48% with half of the probe in contact with the inactive xylem; for *Anacardium*, the underestimation was 17%, with 10% of the probe in contact with the inactive xylem (Clearwater et al., 1999).

In adult trees, the sapwood is approximately 5.0 cm thick (Lemmens, 2008), and the flux density in the radial direction may vary, as observed in *C. alliodora*, *A. excelsum*, *S. morototoni* and *F. insipida* (James et al., 2002), and in the azimuthal direction, as observed in mango (Lu et al., 2000) and cypress (Oren et al., 1999). Indeed, the occurrence of systematic errors (from -90 to +300%) is frequent in the integration of sap flux in a single point in adult trees, because a uniform flux in the radial direction of the trunk is assumed (Nadezhdina et al., 2002).

The estimated LA decreased by 10.8% between the intervals of monitoring (11.95 m^2 - Nov/2014; 10.66 m^2 - May/2015). In comparison to the leaf area of the reference tree from the commercial plantation with the same age, the leaf area was three times smaller in the trees of the lysimeters.

The limitation in the increase of LA, compared with individuals at the field, demonstrates reflexes of root confinement. Netto et al. (2006) observed reduction in the leaf area of young plants of *Coffea canephora* P. under root system confinement. In cases of root limitation, the reduction in shoot growth is associated with the alteration in the electrical conductivity of the root system by the physical impairment and in the concentration of phytohormones responsible for the control of stomatal closure, indirectly reducing the rates of net assimilation and transpiration (Figueiredo et al., 2014).

The T_{SF} showed mean reduction of 57.1% between the first and second evaluation periods (Figure 4), with strong correlation with leaf area (0.77). It is observed that the ET_{PM} and transpiration exhibited significant correlation, but with weak fit indicators (Table 1). Transpiration depended on plant growth, time and existence of uncontrolled factors, such as the effect of advection (Campeche et al., 2011).

In the proposed situation, with maximum water availability of the soil, the lack of adequate response of the plants to the atmospheric evaporative demand is attributed to the root confinement, since Albuquerque et al. (2013) found a rapid positive response in transpiration and other variables related to the gas exchanges of African Mahogany to the water availability.

The reduction in transpiration rate was possibly influenced by the progression of the root confinement, because it can reduce the hydraulic conductivity and, consequently, the water absorption rate of the root system. Reichert et al. (2007) justify that the absorption of water and nutrients by the roots is compromised under physical limitations, because they reduce the production of new roots responsible for the higher absorption rate. Figueiredo et al. (2014) found reduction in transpiration of about 44% in young Eucalyptus plants subjected to root deformations combined with the lower stomatal conductance.

The root system probably reached the water table of the lysimeter, causing physiological disorders related to the lack of aeration in the root zone. Indeed, in the last month of evaluation, emergence of fine roots was observed on the surface of the lysimeter, intended for the action in the processes of water absorption and maintenance of the transpiration flow, compensating the reduction of activity in the root zone subjected to low O_2 availability. The reduction in O_2 concentration in the rhizosphere is a limiting factor for the

Table 1. Linear coefficient, determination coefficient (R^2) and intercept of linear regressions with regression coefficients of the measurements of transpiration (T_{SF}) as a function of the reference evapotranspiration (ET_{PM}), leaf area (LA) and evaluation time (TEv) in young plants of African Mahogany (period Oct/11-Nov/23/2014 and Feb/28-May/10/2015)

Factor	Linear coeff.	R^2
Intersection	2.53^{ns}	0.18^*
ET_{PM}	3.37^*	
Intersection	18.15^*	0.54^*
ET_{PM}	0.91^{ns}	
TEv	-0.06^*	
Intersection	-85.20^*	0.60^*
ET_{PM}	0.83^{ns}	
LA	8.61^*	
Intersection	-133.90^*	0.60^*
ET_{PM}	0.93^*	
LA	12.60^{ns}	
TEv	0.03^{ns}	

^{ns}Not significant; *Significant at 0.05

performance of the metabolic processes of the plants (Queiroz-Voltan et al., 2000), interfering with root permeability (Pelacani et al., 1995).

Conclusions

1. The Granier model underestimates by 44% the daily transpiration of African Mahogany, having the adjusted model $F = 268.25 \cdot k^{1.231}$. Sapwood area is adequate for the estimation.

2. The transpiration of African Mahogany from the age of 2.5 years on, under the imposed conditions, was on average 13.7 L d^{-1}.

3. African Mahogany transpiration directly responded to the atmospheric water demand; however, due to root confinement, it showed signs of dependence on the vegetative growth and on factors not controlled in this experiment.

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