



Sap flow and transpiration of young Brazilian mahogany plants submitted to soil water potential variation

Fluxo de seiva e transpiração de plantas jovens de mogno brasileiro submetidas à variação potencial de água no solo

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Brazilian mahogany (*Swietenia macrophylla* King) is a forest species of economic and environmental interest due to its wood's great finish and its use in recovering and recomposing ecosystems. However, clarification on how this species uses water resources is still necessary. This study proposes to evaluate sap flow and transpiration behavior in young Brazilian mahogany plants under variable conditions of soil water potential. We conducted the study in a protected environment and cultivated the plants in weighing lysimeters wherein the soil underwent potential variations between -10 kPa and -35 kPa during periods of water restriction, rehydration, and full irrigation. To quantify water use in the mahogany plants, we measured sap flow through heat pulses, transpiration through the weighing lysimeters, and evapotranspiration by weather variables. Sap flow and transpiration are affected negatively by soil water potential variation. The leaves lost water to the atmosphere under water deficit conditions, even with the absence of upward sap flow. Sap flow was restored four days after irrigation had resumed.

Keywords: *Swietenia macrophylla* King, heat pulse, rehydration.

O mogno brasileiro (*Swietenia macrophylla* King) é uma espécie florestal de interesse econômico e ambiental, devido a madeira de ótimo acabamento e sua utilização na recuperação e recomposição de ecossistemas, entretanto, o conhecimento de como essa espécie utiliza os recursos hídricos ainda necessita de esclarecimentos. Diante disso, objetivou-se avaliar o comportamento do fluxo de seiva e da transpiração em plantas jovens de mogno brasileiro sob condições variáveis de potencial de água no solo. O estudo foi desenvolvido em ambiente protegido com plantas cultivadas em lisímetros de pesagem, cujo solo em seu interior sofreu variações potenciais entre -10 kPa a -35 kPa em períodos de restrição hídrica, reidratação e irrigação plena. Para quantificar o uso de água no mogno mensurou-se o fluxo de seiva por pulso de calor, a transpiração por lisímetros de pesagem e a evapotranspiração por variáveis temporais. O fluxo de seiva e a transpiração são influenciados negativamente pela variação potencial de água no solo. Ocorreu perda de água das folhas para a atmosfera em condições de déficit hídrico, mesmo com ausência de fluxo de seiva ascendente. O fluxo de seiva foi reestabelecido após quatro dias da retomada das irrigações.

Palavras-chave: *Swietenia macrophylla* King, pulso de calor, reidratação.

1. INTRODUCTION

The Brazilian mahogany (*Swietenia macrophylla* King) is a native species of Brazil, belonging to the Meliaceae family that can reach 45 m in height and 2 m in diameter [1]. Its wood has economic importance due to its durability and excellent finish when used in the manufacture of luxury furniture, decorative items, musical and precision instruments [2, 3]. In Brazil, its economic exploitation was reduced due to the incidence of the mahogany drill (*Hypsipyla grandella* Zeller), however it is indicated in reforestation areas, mainly because of its accelerated growth [4, 5].

One of the most important physiological attributes of trees is transpiration, which participates in approximately 99% of the water transferred from the plant to the atmosphere daily, and this process is directly correlated with the sap flow. The sap flow participates of water storage in the stem, redistribution and photosynthesis in leaves, i.e., the understanding of the sap flow is essential to infer about the transpiration behavior in trees [6, 7].

There are several methods that correlate transpiration with sap flow and have been used in research concerning the use of water by plants, such as the thermal dissipation method [8, 9], the heat equilibrium method [10, 11] and the heat pulse velocity method, mainly the heat ratio method, initially proposed by [12] and later improved by [13]. This method has advantages over other methods, as it allows the measurement of low (slow) and reverse (negative) flows [14, 15], which helps in the correct determination of the percentage of sap flow that is destined for rehydration and redistribution in the root system.

However, sap flow determination methods have restrictive methodological, such as incomplete probe to stem contact, natural temperature gradients (NTG), species specific parameters, uncertainty in baseline sap flow, effects of injury and sensor deviation [16] which leads to the need for further studies on the feasibility of using this is methods in conditions under adverse development conditions, such as potential variation of water in the soil.

It is known that the soil water potential directly and indirectly influences the factors that govern the movement of water in the plant, such the storage, sap flow and gas exchange, constituting an important parameter for understanding the relationship water-soil-plant-atmosphere and how species deal with the dynamics of water in the environment [17-19].

Given the above, this study aimed to evaluate the behavior of sap flow and transpiration in young Brazilian mahogany plants under varying conditions of soil water potential.

2. MATERIAL AND METHODS

The study was conducted in a protected environment located on the premises of Nucleus for Water Engineering on the Soil (NEAS) of the Federal University of Bahia Recôncavo (UFRB), Cruz das Almas, Brazil. Were used eighteen-month-old Brazilian mahogany plants cultivated in weighing lysimeters per load cell. The lysimeters recorded the variation of mass in the soil, resulting from the processes of transpiration and replacement of water in the soil (irrigation).

During periods of water replacement, irrigations were carried out daily, aiming to raise the soil water potential to -10 kPa, considered the theoretical moisture potential in the field capacity. A representative lysimeter, without plant, was used to convert the mass changes in the lysimeter into soil water potential by means of inverse modeling, where the hourly soil water content (Θ) measured by Time-Domain-Reflectometry (TDR) and the hourly evaporation measured in the weighing lysimeter, were used in the HYDRUS - 1D software. Through this software, solved the eq. 1 by [20] for estimating soil water flow:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left[K(\theta) \left(\frac{\partial h(\theta)}{\partial z} - 1 \right) \right] \quad (1)$$

where h is the soil water pressure (m H₂O), Θ is the soil water content (m³ m⁻³), t is the time (h), z is the vertical coordinate (m) and $K(\Theta)$ represents the soil hydraulic conductivity function (m h⁻¹).

The model of Mualem-Van Genuchten [21, 22] was used to describe the soil water retention curve (SWRC) and the soil water conductivity curve (SWCC). The SWRC is described by eq. 2 and SWCC described by eq. 3:

$$\begin{cases} \theta(h) = \theta_s & h \geq 0 \\ \theta(h) = \theta_r + (\theta_s - \theta_r) \left[\frac{1}{1 + |\alpha h|^n} \right]^{(1-\frac{1}{n})} & h < 0 \end{cases} \quad (2)$$

$$K(\theta) = K_s S_e^\lambda \left[1 - \left(1 - S_e^{\frac{n}{n-1}} \right)^{1 - \frac{1}{n}} \right]^2 \quad (3)$$

where S_e is the effective saturation, defined as $S_e = (\Theta - \Theta_r) / (\Theta_s - \Theta_r)$; Θ_r and Θ_s the residual and saturated water content ($\text{m}^3 \text{m}^{-3}$), respectively; h is pressure ($\text{m H}_2\text{O}$), $K(\Theta)$ and K_s the soil hydraulic conductivity and saturated soil hydraulic conductivity (m h^{-1}), α (m^{-1}), n e λ are empirical parameters.

The soil hydraulic parameters (α , n , λ and K_s) were determined by minimizing the observed Θ differences (obtained by TDR) and simulated in space-time. Thus, the total of differences obtained between observed and simulated values of Θ was expressed by an objective function, Φ , defined as:

$$\Phi(\theta, \beta) = \sum_{j=1}^m \sum_{i=1}^{n_j} [\theta_{TDR,j}(z_i, t_i) - \theta_{PRED,j}(z_i, t_i, \beta)]^2 \quad (4)$$

where, the right side of eq. 4 represents the residue between the soil water content observed in the TDR (Θ_{TDR}) at time t_i for j_{th} measured in z_i , and the corresponding estimated soil water content values (Θ_{EST}) using the soil hydraulic parameters optimized in β (i.e., Θ_r , Θ_s , α , n , K_s e λ); m is the number of different measurement locations of Θ ; and n the number of measurements performed in one m . The minimization of the objective function Φ is performed using the Levenberg-Marquardt nonlinear minimization method. With the statistical indicators resulting from the minimization of eq. 4 to obtain Θ_r , Θ_s , α , n , K_s and λ (eqs. 2 and 3), the soil water potential values were estimated daily.

In the quantification of the sap flow (SF) the heat pulse by the heat ratio method (HRM) of [13], was used as described [23] and [24]. Based on this method, sets of probes were built comprising 2 T type thermocouple probes, to quantify the temperature variation upstream and downstream of the heat source, and 1 probe to generate an intermittent heat pulse, with dissipated power of 2.4 W every 10 minutes, enough to change the temperature of the sap flow by 2.8°C. A Campbell Scientific® model CR1000 datalogger was used to excite and measure temperature variations in the probes set, as well as store the $\ln(v_1/v_2)$ ratio at hourly intervals. The thermocouple probes was installed in 3 plants of 18 months of age, cultivated weighing lysimeters, similar to studies carried out by [25]. in addition, a plant was used to determine the properties of the sapwood, as this is a destructive analysis. More details on weighing lysimeters, probes construction, method calibrations and uncertainties involved in sap flow measurement in *Swietenia macrophylla* King were published in a previous study by [26].

Figure 1 shows details of the constructed probes and the lysimeters used in the experiment.



Figure 1. Heating probe (a), T type thermocouple (b), set of probes installed in the stem (c) and weighing lysimeter (d).

The evaluations took place between July 13 and August 04 of 2018 and the plants were submitted to variable conditions of water potential in the soil, characterized as: (1) period of water restriction (July 13 to July 23), in which irrigation was suspended to provoke continuous negative variations in soil water potential until the upward sap flow ceased; (2) period of rehydration (July 23 to July 30), in which irrigations was resumed and soil water potential was raised to close to the theoretical limit of field capacity (-15 kPa) and (3) period of full irrigation (July 30 to August 04) where daily irrigations were carried out, with soil water potential varying around -10 and -15 kPa.

For a better understanding of the collected data, figures were generated that express the variations in soil water potential and sap flow, for each evaluation period; the curves of ascending sap flow ($FS > 0$), inverse sap flow ($FS < 0$) and transpiration during the study period; the difference between accumulated sap flow and transpiration over time and the segmented linear regressions that correlate the sap flow and transpiration normalized by reference evapotranspiration (E_{to}) with the soil water potential.

The evapotranspiration was calculated by the Penman-Monteith method, following instructions contained in FAO Bulletin 56 for protected environment conditions and missing data [26]. The temporal variables measured were air temperature ($^{\circ}\text{C}$) and relative humidity (%) by a thermohygrometer model HC2S3 from Campbell Scientific® and radiation (MJ m^{-2}) by a pyranometer model LP 02 from the manufacturer Hukseflux®.

3. RESULTS AND DISCUSSION

In the period of water restriction, the sap flow progressively decreased in response to the continuous reduction of the soil water potential (Figure 2).

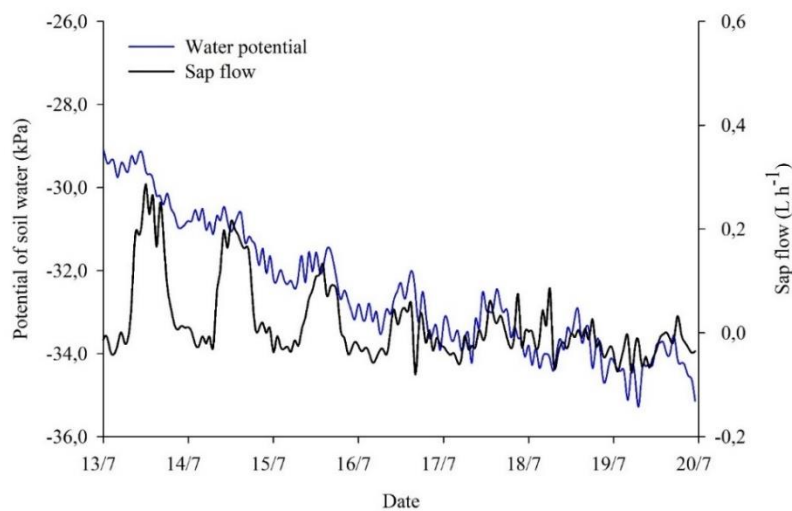


Figure 2. Variation of sap flow in response to the reduction of soil water potential in the period of water restriction.

The existence of negative (reverse) sap flow was observed throughout the period, being more pronounced from the day July 16 when the water potential in the soil became less than -32 kPa, resulting in practically zero upward flow below this value. The results show that soil moisture governed the sap flow variation in Brazilian mahogany due to a tendency to decrease or increase sap flow following changes in soil water (reduction of moisture or rehydration). Tendencies and expressive positive correlations between soil water content and sap flow are best discussed in studies of [27]. When water availability is limited, plants are confronted by the surrounding high osmotic potential, resulting in loss of initial turgor in the root system due to the combination of signaling and adjustment [28]. Furthermore, only the reduction of soil water content is sufficient

to affect root water uptake and trigger negative physiological responses such as reduction sap rates and stomatal conductance in order to conserve water and avoid critical water potentials that would result in hydraulic failure (such as cavitation and subsequent embolism), in addition to negative sap flow regulation [29-31].

On day July 23 the soil water potential was elevated from -35 kPa to close to -15 kPa and maintained until the end of the study. On the first night of the rehydration period, the highest reverse flow intensity of the entire period was observed (Figure 3). This occurs because of the variation in the availability of water in the soil, the increase of which allowed, firstly, the rehydration of the root system and then the aerial part of the plant, as only an ascending flow was observed at night between July 26 to July 28.

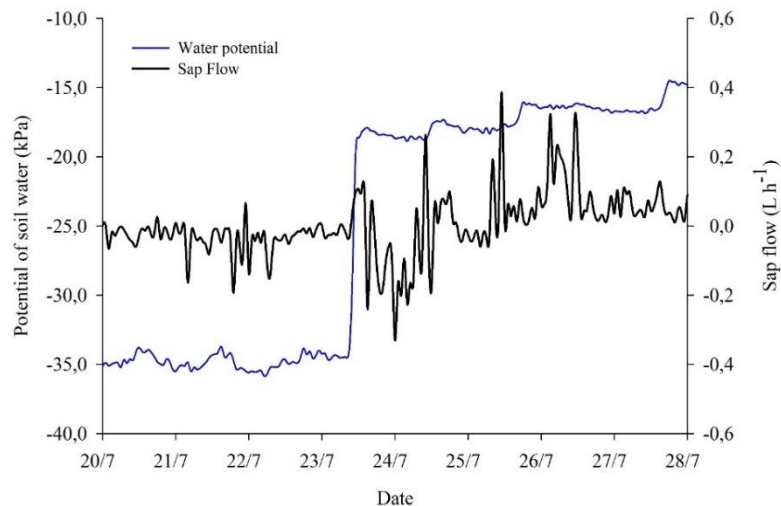


Figure 3. Variation of sap flow in response to plant rehydration after the period of water deficit.

It was also observed that after the increase in the soil water potential, there was abscission of the older leaves, as a result of a physiological mahogany strategy aiming to maintain essential processes, such as the maintenance of the turgor of new leaves and the water recharge in stem.

Physiological and genetic responses demonstrate that the initial reaction of plants to drought is due to the role of electrical and/or hydraulic signals emitted from the roots to the leaves, resulting in increased local water potential and increased tension in the xylem vessels, which will be relayed to the aerial part [32, 33] which can cause variation in sap flow and leaf abscission.

The increase in hydraulic conductivity of *Argania spinosa* roots under water restriction and after a short period of rehydration was reported by [34], demonstrating that it is a physiological response of the root as a drought recovery strategy. The phenological status and age of leaves were also considered biotic factors that determine leaf abscission and sap flow variation in *Quercus variabilis* in a study reported by [35], in addition, the leaf petiole works as a hydraulic fuse and is indicated as the organ that defines the maximum stress supported by a plant under water stress conditions [31]. In olive plants under water deficit, the negative regulation of the stomatal conductance of the leaves favored the hydraulic functioning of the stem [36]. These findings reinforce the results shown that Brazilian mahogany modulated the direction of sap flow and leaf loss to favor the water dynamics between the root and stem components.

With the elevated in the soil water potential, the sap flow ascending and reverse was reestablished 4 days after irrigation (July 30 to August 04) (Figure 4). Similar to this result, Albuquerque et al. (2013) [37] submitted *Khaya ivorensis* to 14 days of water restriction and verified the recovery capacity of leaf water status and gas exchange in 3 days after the resumption of irrigation.

It is important to point out that the occurrence of nocturnal ascending flows in subsequent days indicates the period of reestablishment of the mahogany sap flow after the hydric stress event (Figure 4). The occurrence of nocturnal sap flows is necessary for the hydraulic functioning of

the plant, as it affects the balance in the relationship between the soil-plant water potential in the predawn, with consequences for field methodologies that measure water stress in plants [38]. Thus, the quantification of ascending and reverse flows from day July 30 demonstrates the normalization of sap flow in mahogany after the beginning of the rehydration period.

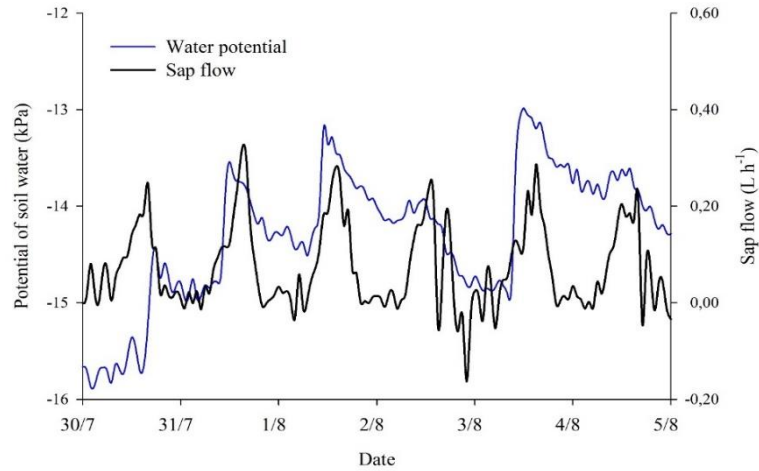


Figure 4. Reestablishment of sap flow after elevated soil water content.

Figure 5 shows the positive sap flow ($FS > 0$), the negative sap flow ($FS < 0$) and transpiration during the entire period observed. The occurrence of transpiration is noted even with positive sap flow close to zero in the period of water restriction, and this behavior is possible due to the loss of water from leaf tissues to the atmosphere without rehydration from the stem by sap flow due to the height of the plant. More refined studies show that low soil water contents generate hydraulic dysfunction and change in plant water status, that is, xylem hydraulic dysfunction drives whole leaf hydraulic decline, with consequent leaf dehydration and damage, sometimes irreversible, such as loss of rehydration capacity or turgidity [39-41].

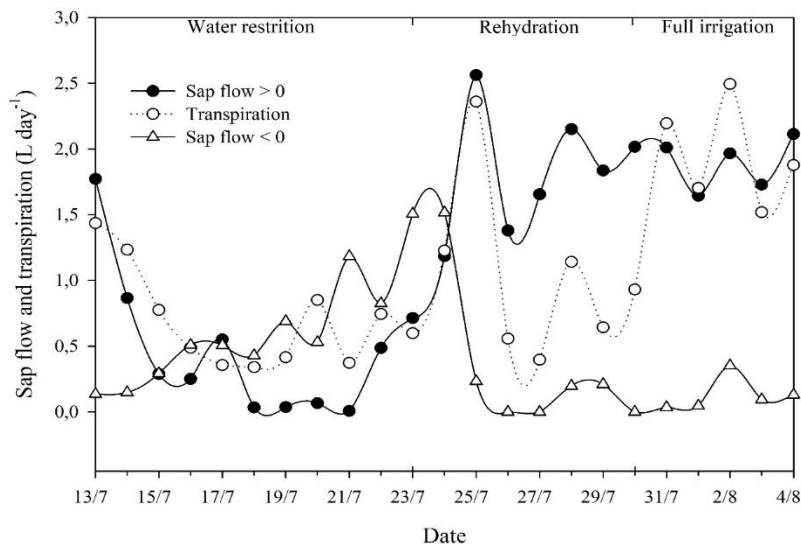


Figure 5. Mahogany sap flow and transpiration over time.

After irrigation on July 23, the ascending sap flow approached the transpiration values, surpassing it later, however, due to the occurrence of leaf abscission between 25 and 27 of July,

the SF cannot be associated with transpiration, only demonstrate that this was on average 2.0 L day^{-1} while $FS < 0$ was close to zero. From July 31, during the period of full irrigation, there was a good association between $FS > 0$ and transpiration due to the maintenance of soil water potential close to field capacity. These results are important as they show that sap flow data should be used with caution when associating it with transpiration, because the variation in soil water potential is responsible for several physiological changes in plants.

It should be noted that the reduced period of analysis of the response of *Swietenia macrophylla* King was not compromised due to the water memory to drought (variation of water in the soil), since the plants develop strategies to circumvent subsequent stressful events [42, 43].

The influence of soil water potential on the sap flow and transpiration components, normalized by the reference evapotranspiration, is shown in Figure 6. In both physiological processes variations were observed for potentials below a critical limit of -27.8 kPa , approximately 15% in sap flow and 5.4% in transpiration, for each increment of soil water potential. Between the critical limit of -27.8 kPa to -32.2 kPa , the sap flow corresponds, on average, to 0.678 L mm^{-1} of E_{to} and the transpiration to 0.551 L mm^{-1} of E_{to} . The soil water potential at which the Brazilian mahogany sap flow becomes reversed ($FS < 0$) corresponds to that less than -32.2 kPa .

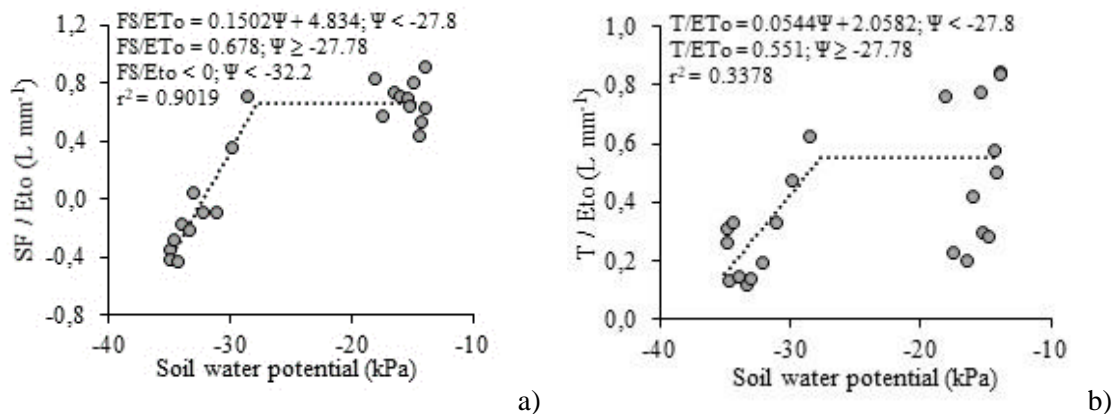


Figure 6. Relationship of the ratio of sap flow and evapotranspiration to soil water potential (a) and transpiration and evapotranspiration to soil water potential (b) throughout the evaluation period.

Knowledge of planting technologies and monitoring of forest species such as the Brazilian mahogany is still incipient, and this critical limit of water potential in the soil can help researchers and producers in the strategies for inserting this species in the recovery of degraded areas, in cultivation in regions with water deficit, in agroforestry systems and also in the production of seedlings, as it is an important parameter for the quantification of the water demand.

4. CONCLUSION

The sap flow and transpiration in Brazilian mahogany are influenced by soil water variation, mainly below a critical limit of -27.8 kPa to -32.2 kPa , when the sap flow is null.

Under conditions of low soil water potential, with variations close to -35 kPa , transpiration occurred in Brazilian mahogany even with the absence of ascending sap flow, due to the loss of water from leaf tissues to the atmosphere.

Brazilian mahogany reestablished sap flow four days after elevated soil water potential.

5. ACKNOWLEDGMENTS

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