

RELATIVE CONTRIBUTION OF NIGHTTIME TRANSPIRATION TO TOTAL WATER USE IN FOUR WOODY SPECIES ALONG AN ALTITUDINAL GRADIENT AT THE ATLANTIC RAIN FOREST

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INTRODUCTION

Several studies have shown that nighttime transpiration (NTE) is a common process in several species from contrasting environments (Dawson *et al.*, 007) and might represent as much as 50% of total daily water loss. (Dawson *et al.*, 007). The functional significance of this process is not completely understood and the following hypotheses have been proposed to explain the occurrence of this phenomenon: NTE increases oxygen supply, which is necessary to sustain respiration in xylem parenchyma; it might a consequence of incapacity of complete stomatal closure; NTE facilitates bulk flow of water to the roots overnight, promoting nutrient uptake what could promote niche partitioning.

Nocturnal vapor pressure deficit (VPD) is considered the most important force driving nighttime transpiration (Dawson *et al.*, 007). Few studies have been conducted in tropical rain forests to report the occurrence of nocturnal transpiration (Dawson *et al.*, 007) and its role in whole plant water use. Tropical rain forests are characterized by high environmental heterogeneity and high species diversity (Myers *et al.*, 000), therefore, studies investigating nocturnal transpiration should take into account the consequences spatial and temporal heterogeneity of environmental factors as controlling variables of species ecophysiological responses.

The Atlantic Forest occurs along the Brazilian coast and is considered a hot - spot in terms of biodiversity and endemism (Myers *et al.*, 000). This biome is a mosaic of ecosystems that belongs to the Atlantic Domain and includes areas of coastal flooded forest, lowland and montane tropical rainforests. Along altitudinal gradients, as observed in the Atlantic rain forest, directional changes in abiotic factors, such as increases of radiation and decreases in temperature and atmospheric pressure, and the presence of fog in montane forests, can affect the responses of plant species in different ways (Körner, 2007). The species responses along altitudinal gradients have been studied especially in a morphological level and most studies on water relations of tropical rain forest trees were performed in lowland tropical rainforests. Morevover, because VPD is the major force driving nocturnal transpiration, not only the variation between sites will be relevant, but also, how expose is the crown to atmosphere.

In general, tropical understorey plants do not show variations in transpiration fluxes even when variations in stomatal aperture are taken into account, leading these species to slower responses to changes in the atmospheric conditions when compared to overstorey species (O'Brien *et al.*, 004). Thus, variations in stomatal aperture can have a small relevance to transpiration because, the sum of boundary layer conductances of all the plants would have a strong contribution to the magnitude of the fluxes.

Along altitudinal variations the presence of fog at the Montane Forests cause decreases on radiation received, what, consequently, reduces photosynthetic rates and and transpirational fluxes (Graham *et al.*, 005). However, reduced water losses could be advantageous even for plants ocurring in Montane Forests because some factors such as low partial pressure of CO_2 , low wind velocity and high solar radiation (during fogless periods) due to lower turbidity of atmosphere tend to drive plant to loss more water in high altitudes (Körner, 2007).

We hypothesized that nocturnal transpiration for understorey species will be more similar between altitudes (because of the buffering capacity of microclimatic conditions), contrary to expected to overstorey species.

OBJECTIVES

We addressed the following questions: What are the most important factors that drive nighttime transpiration? The crown exposure or the altitude? What are the seasonal dynamics of NTE?

MATERIAL AND METHODS

3.1 - Study sites and species

The measurements were made in lowland and montane forest in the Serra do Mar State Park, which covers 315,000 hectares and is located north of the state of São Paulo, Brazil.

In the lowland rain forest - 100 m above sea level - $(23^{\circ} 31' \text{ to } 23^{\circ} 34' \text{ S} \text{ and } 45^{\circ} 02' \text{ to } 45^{\circ} 05' \text{ W})$ the climate is tropical without a marked dry season with a mean annual precipitation of 2.200 mm. The driest months are normally july and august. In the montane forest - 1000 m above sea level - $(23^{\circ} 17' \text{ to } 23^{\circ} 24' \text{ S} \text{ and } 45^{\circ} 03' \text{ to } 45^{\circ} 11' \text{ W})$ the climate is tropical temperate, without a marked dry season with mean precipitation annual superior to 2.000 mm. All physiognomies are characterized as broad leaf evergreen.

We selected four species according to three criteria: co - occurrence in both sites, canopy position and species belonging to different families to avoid phylogeny effects. Thus, the following species were chose: *Hyeronima alchorneoides* Allemão (Phyllantaceae), *Alchornea triplinervea* (Spreng.) Müll. Arg. (Euphorbiaceae), *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae) and *Rustia formosa* Klotzch (Rubiaceae). For simplicity, we will refer to each species by their generic names. Hyeronima and Alchornea it is among the tallest trees at the study sites and can reach 30 m. Mollinedia it is a understory tree with most individuals having heights between 5 and 7 meters. and Rustia are mid - canopy species with a mean height of 14 and 17 m, respectively.

3.2 - Sap - flow probe installation and measurements

We used the heat ratio method (Burgess et al., 001) to make continuous measurements of sap flow in trunks of our study species. The HRM is basically to measure the increase in temperature following a heat pulse at two symmetrical points, above and below a heater inserted 6 mm into the active sapwood. This technique allows bi - directional measurements of sap flow and also measures very slow flow rates. One heater and a pair of copper-constantan thermocouples were inserted into the xylem tissue of the trunks at breast height of three individuals per species. Each thermocouple had two junctions to measure sap velocity at two depths in the xylem tissue. Standard needles are 35mm long and have two thermocouples located 7.5 mm and 22.5 mm from the tip of the needle. This provides a spacing of 15 mm between each thermocouple and a 12.5mm distance between the outer thermocouple and the epoxy base of the needle. The 15 mm spacing between thermocouples is to prevent thermal contamination of the readings. A metal guide (with three holes carefully drilled on a parallel line, spaced out 6 mm apart) was used to help drilling holes and minimize probe misalignment during insertion. The heater was set up to send a pulse every 30 min and temperature ratios were recorded continuously with a data logger (ICT, Australia). We calculated the heat pulse velocity (Vh; cm hr) as:

Vh = (kX - 1) x ln (v1 (v2) - 1) x 3600

where k is the thermal diffusivity of the fresh wood, X is the distance between the heater and the thermocouples, and v1and v2 are the differences between the initial temperature at the two thermocouples (downstream and upstream the flow in relation to the heater, respectively) and the temperature measured after a heat pulse. The measurements were done during a rainless period of one month. The nighttime transpiration was expressed as expressed as % of daylight maximum transpiration rate (En) of thirty days and we considered data made between 22:30 and 04:30 h. The figures considering absolute values and % contribution of nighttime contribution in 24 hours included only the two last weeks of the rainless period.

3.3 - Environmental variables

We placed three air temperature and relative humidity (HOBO) at different heights (2, 7 and 15 meters) in each site. Data were collected every 30 min and were used to calculate the vapor pressure deficits (VPD, kPa).

RESULTS AND DISCUSSION

During the rainless period there were differences of nighttime transpiration between the forests. At the lowland site, Hyeronima (the tallest species) was the only one that showed a non - linear relationship between En and VPD where the En reached 60% of daylight maximum transpiration rate ($R^2 = 0.91$; p < 0.001), while Alchornea ($R^2 = 0.54$; p < 0.05), Rustia (R²=0.54; p < 0.05) and Mollinedia $(R^2=0.62; p < 0.05)$ reached values around 30%. Nocturnal VPD was higher in the Montane forest reaching values close to 0.6 kPa against values close to 0.2 kPa in the Lowland forest. In the montane forest, Alchornea and Mollinedia also showed a high nighttime transpiration (close to 60%) in comparison to lowland forest. Only Rustia did not show increases in En at the Montane site, however, the slopes were different between sites. The non - linearity occurred only for the tallest species (Hyeronima and Alchornea) in the Montane forest. Thus, considering each site separately, all species showed the same behavior even occupying different positions through the canopy, however, the magnitude of transpirations were different.

After rainfall, there were no relationship between nighttime transpiration and VPD at the lowland Forest, indicating xylem refilling. At the Montane site the nocturnal VPD was higher than at Lowland (0.6 and 0.2 kPa, respectively). Hyeronima and Alchornea showed a non linear relationship between En and VPD, both reaching values close to 60% $(R^2=0.75 \text{ and } R^2=0.66; p < 0.05, respectively)$. The relationship between En and VPD was linear for Mollinedia and Rustia ($R^2=0.46$ and $R^2=0.86$; p <0.05, respectively). Contrary to observed at the Lowland Forest, there were relationship between En and VPD after rainfall for all species. Hyeronima continue to show high values (60%; $R^2=0.75$; p <0.01) while Alchornea reached values near 50% (R²=0.66; p < 0.05). Mollinedia and Rustia reached values close to 10% (R²=0.30 and R²=0.54; p <0.05, respectively). The increase of rain and fog events could be associated to the lower En after rainfall (Graham et al., 005). The nonlinear relationships are possible explanations to stomatal restrictions. Higher stomatal restrictions minimize the water

losses caused by high radiation, high VPD and the lower atmospheric pressure (Sperry *et al.*, 002), leading all the species, independently of their crown exposure, to respond in a similar way at the Montane site. At the Lowland Forest, radiation, VPD and high atmospheric pressure do not drive great amount of water loss and for that, only *Hyeronima*, that is the tallest species and has the crown fully exposed, showed stomatal restrictions.

CONCLUSION

Crown exposure does not seem to be the most important factor affecting nighttime transpiration, but the variation of atmospheric conditions according to the altitude. In addition, our findings that the En can reach 60% indicates that this process might have a significant role in the water balance of these forests.

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