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Diversity in nighttime transpiration behavior of woody species of the Atlantic Rain Forest, Brazil

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ABSTRACT

Nighttime transpiration (NT) has been documented in many plant species but we do not yet have a thorough understanding of the abiotic and biotic controls of this phenomenon. In this study we examined interspecific variation in NT behaviors in plants with distinct crown exposures (CE) and occurring at lowland (100 m) and montane forests (1000 m) in the Brazilian Atlantic rainforest to answer the following questions: are there different NT behaviors in plants subjected to distinct conditions associated with degree of CE and/or altitude? Are there higher rates of NT relative to daily maximum values at the montane forest due to higher vapor pressure deficit (VPD)? Taking into account that low VPD should generally produce low relative NT fluxes, should we expect that understory species in both altitudes will have quite uniform low relative rates of NT in comparison to overstory species owing to the buffered nature of within-canopy microclimate? NT did show differences between altitude and species. Of most significance was a prominent non-linear relationship between the NT and VPD, observed at the montane site. This non-linearity is in contrast to most previously published NT kinetics and suggests stomatal and/or leaf energy balance controls on NT. Our findings raise a new perspective concerning thermodynamic contributions to non-linear RT kinetics and some possible reasons for this interesting behavior are discussed.

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1. Introduction

Transpiration by plants follows a force–flux relationship that is shaped by the ability of a plant's transport system to conduct water. Plants can modify their hydraulic conductivity throughout the entire transport system and perhaps the strongest and most dynamic control is that of stomatal aperture which affects conductance to water vapor: understanding stomatal behavior in response to environmental conditions is thus key to understanding variation on plant water fluxes (Cowan and Farquhar, 1977; Jones and Sutherland, 1991; Cruiziat et al., 2002). A commonly known relationship between transpiration and vapor pressure deficit (VPD) shows a non-linear saturating response of daytime transpiration to VPD because of decreases in stomatal conductance in response to a drying atmosphere (Jones and Sutherland, 1991; Cruiziat et al., 2002). While daytime transpiration dynamics are

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quite well studied, nighttime transpiration (NT) has only recently become an important research subject.

NT has been described for guite a few plant species from contrasting environments (Donovan et al., 2001; Dawson et al., 2007; Snyder et al., 2008; Christman et al., 2008; Novick et al., 2009) and while generally lower in magnitude relative to daytime transpiration, it is none-the-less significant enough for potential impacts on whole-plant water relations and ecosystem hydrology (Dawson et al., 2007; Wood et al., 2008). Functional consequences of NT include pre-dawn disequilibrium, increases in oxygen supply (Daley and Phillips, 2006) and facilitation of bulk flow of water to the roots overnight which may promote nutrient uptake (Donovan et al., 2001; Snyder et al., 2003). Although little is known about the controls of NT, a strongly linear positive relationship between sapflow and VPD has been documented in several ecosystems, suggesting that VPD is the most important environmental driving force for nocturnal water loss and that the crown conductivity is constant (Fisher et al., 2007; Dawson et al., 2007).

In tropical forests, small-scale changes in abiotic factors such as VPD, air temperature and solar radiation are common due to the large heterogeneity of canopy structure, topography and wind patterns (Motzer, 2005). Thus, even in short horizontal and altitudinal distances, plant species may be subjected to high

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spatio-temporal heterogeneity (Leigh et al., 2004). In view of the large heterogeneity in tropical forests, many studies have been performed to evaluate species responses at different scales (Bruijnzeel and Veneklaas, 1998; Velázquez-Rosas et al., 2002; Graham et al., 2005; Holder, 2007; Beaumont and Burn, 2009; Poorter, 2009). Species responses along altitudinal gradients have been studied especially at a morphological level (Bruijnzeel and Veneklaas, 1998; Velázguez-Rosas et al., 2002; Holder, 2007; Rosado et al., 2010) where species from contrasting environments exhibit different leaf morphologies in response to the degree of crown exposure (CE) and the environmental regime this implies (Poorter, 2009). To date however, whole plant water relations of tropical rain forest trees have not been examined along altitudinal gradients (Santiago et al., 2000, 2004; Oliveira et al., 2005a). It is equally true that the science surrounding NT has been poorly advanced in tropical rain forests (Dawson et al., 2007). Since tropical rain forests present high environmental heterogeneity and high species diversity (Myers et al., 2000; Leigh et al., 2004), this is both a major hindrance and major research need for understanding how nighttime conditions affect plant ecophysiology and overall forest function.

The Atlantic Forest occurs along the Brazilian coast and is considered a biodiversity hot-spot (Myers et al., 2000). This biome is a mosaic of ecosystems that belongs to the Atlantic Dominion including lowland and montane forests (Joly et al., 1999). In addition, altitudinal gradients present in the Atlantic rain forest produce directional changes in abiotic factors such as increases in solar radiation and VPD (Rosado et al., 2010) and decreases atmospheric pressure (Rosado, 2011). These changes promote strong directional changes in plant traits such as increases in leaf longevity and decreases in transpiration (Grubb, 1977; Bruijnzeel and Veneklaas, 1998; Leuschner, 2000; Körner, 2007).

Considering the high environmental heterogeneity that tropical forest plants are subjected to via vertically complex canopies and altitudinal variation, we chose four woody species from Atlantic Rainforest co-occurring in Lowland (100 m) and Montane forests (1000 m) and occupying different canopy strata to answer the following questions: are there different nocturnal transpirational behaviors in plants subjected to distinct conditions associated with degree of crown exposure (CE) and/or altitude? Taking into account that low VPD should generally produce low relative NT fluxes, should we expect that understory species in both altitudes will have quite uniform low relative rates of NT in comparison to overstory species owing to the buffered nature of within-canopy microclimate? Answering these questions concerning the diversity of NT ecophysiology within Atlantic Rainforest, using sap flow measurements to trace day and nighttime transpiration, will deepen our understanding of the structural and functional complexity of these valuable forests which face threats from fragmentation and shifting environmental conditions.

2. Materials and methods

2.1. Study sites and species

Our study was conducted in lowland and montane forests in the Serra do Mar State Park, covering 315,000 ha in the Atlantic Rain Forest in the north of São Paulo state, Brazil. The Lowland forest is around 100 m above sea level – $(23^{\circ}31'-23^{\circ}34' \text{ S and } 45^{\circ}02'-45^{\circ}05' \text{ W})$ and has a tropical climate and a mean annual precipitation of 2200 mm. Usually, the driest months are July and August. The Montane forest is 1000 m above sea level – $(23^{\circ}17'-23^{\circ}24' \text{ S and } 45^{\circ}03'-45^{\circ}11' \text{ W})$, has a tropical temperate climate, with mean annual precipitation around 2000 mm and fog frequency is around 100 days per year (Rosado et al., 2010). All physiognomies are characterized as broadleaf evergreen tropical forests.

We selected plant species according to co-occurrence at both sites, contrasting canopy position (overstory, intermediary and understory) and species belonging to different families to avoid phylogenetic effects on the study of NT behavior. The species chosen were: *Hyeronima alchorneoides* Allemão (Phyllantaceae), *Alchornea triplinervea* (Spreng.) Müll. Arg. (Euphorbiaceae), *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae); and *Rustia formosa* Klotzch (Rubiaceae). *Hyeronima* and *Alchornea* are overstory species while *Rustia* is an intermediary and *Mollinedia* an understory species. For simplicity, we will refer to each species by their generic names.

2.2. Sap-flow probe installation and measurements

We used the heat ratio method (Burgess et al., 1998, 2001) to make continuous measurements of sap flow in trunks in three individuals per species at each site. The HRM measures the increase in temperature following a heat pulse at two symmetrical points, 5 mm above and below a heater inserted 30 mm into the active sapwood. This technique allows bi-directional measurements of sap flow and also measures very slow flow rates which we might expect during the night. Sap flow sensors (HRM30 ICT International Pty Ltd., Armidale, NSW, Australia) were inserted into the xylem tissue of the trunks at breast height of three individuals per species. The heater was set up to send a pulse every 30 min and temper-



Fig. 1. Mean air temperature ($^{\circ}$ C) of three strata (overstory, intermediary and understory) at the Lowland and Montane forests along the whole period of study. Data collected every 30 min.

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