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Short communication

Curios relationship revealed by looking at long term data sets—The geometry and allometric scaling of diel xylem sap flux in tropical trees

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ABSTRACT

Daily xylem sap flux values (*daily* J_s) and maximum xylem sap flux values (*max* J_s) from 125 tropical trees from different study sites in the Neotropics were compared. A cross species and study site relationship was found between daily and maximum values. The relationship can be expressed as *daily* $J_s = 6.5\ x\ max\ J_s$. The geometrical relationship between the maximum xylem sap flux of a given day is thus defining the daily xylem sap flux rates. Assuming a bell-shaped diurnal sap flux course and a relatively constant day length the maximum xylem sap flux is the only possible changing variable to define daily fluxes. Further, this relationship is showing the inertia of the xylem sap flux as a physical object and highlights the delayed response to environmental changes and its subsequent inevitable susceptibility under environmental stress to hydraulic failure.

Xylem sap flux dynamics and its movement in plants is playing an essential role in understanding plant hydraulic function (Steppe et al., 2015). According to the most widely accepted theory xylem sap flux is moving along a pressure gradient the so called soil–plant–atmosphere continuum. The rate of xylem sap flux is controlled by three variables. First by the gradient of water potential and soil water status, second the plant hydraulic resistance and third the vapor water deficit of the atmosphere. The strong dependency of xylem sap flux on those three variables allows to make some generalizations and to integrate those generalizations into the development of xylem sap flux models (Dierick and Hölscher, 2009; O'Brien et al., 2004). Such process-based plant models are the key for understanding the hydraulic tree functioning in response to internal and external factors by predicting responses of plants to changes in the environment (Fonti and Jansen, 2012; Paudel et al., 2015). Most studies thus focus on the important relationship xylem flux and environment and probably most of the important relationships have already been described, however to my knowledge there is no study looking into the diel variation in shape and size (geometry) or size to shape relationship (allometry) of xylem sap flux. In this study I summarize data from various research sites in the Neotropics and present a cross areal relationship between daily xylem sap flux densities and the maximum observed xylem sap flux density on a given day. The study supports our basic understanding of the mechanistic functioning of the transpiration stream. I further presents empirical data that could be incorporated to mimic daily xylem sap flux performance and justifies gap filling methods in long term xylem sap flux based transpiration estimated.

This study was conducted in two tree plantations in the surroundings of the village of Sardinilla in Panama (9°19′N, 79°38′W) and in a tropical old growth forest as well as in an agroforestry plantation in the Central Amazon, in and outside of the City of Manaus in Brazil (02°38′S 60°09′W). Altogether, xylem sap flux density (J_s, g cm^2 h^{-1}) was measured in 125 trees with 2 cm long Grainer type thermal dissipation probes (Granier, 1985, 1987). Each tree was equipped with a set of two sensors installed at breast height (1.3 m) and in opposite direction in the tree trunk. All sensors were protected and insulated with Styrofoam boxes covered with reflective and plastic foil. In Panama, xylem sap flux density was measured 76 trees from nine different species between June 2007 and July 2008 (for more details on trees species and planting scheme see: Kunert et al., 2010, 2012). In Brazil, xylem sap flux densities were recorded for 49 trees and palm trees from which 3 trees and 3 palm trees were growing in an agroforestry system over the period of two months in 2011 (compare Kunert et al., 2015a, 2013) and the other 39 trees from 35 different species in an old growth *terra firme* forest over the period of one year in 2013 (Kunert et al., 2015b). Sap flux was assessed for another 4 trees in the City Center of Manaus in a private orchard for various days (Kunert and Edinger, 2015; Kunert and Mercado Cardenas, 2012). At all study sites voltage out-

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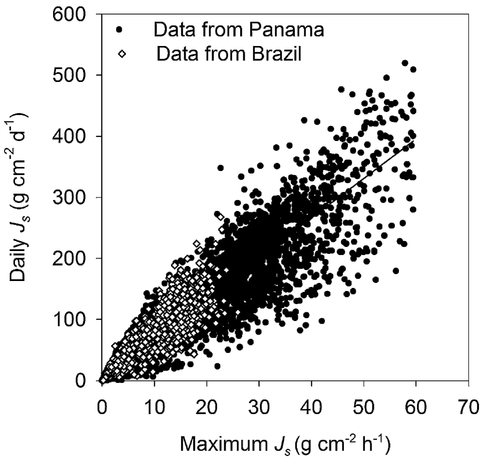

Fig. 1. Liner relationship between daily xylem sap flux and maximum xylem sap flux (n = 125 trees) from different study sites. Solid dots are data from Panama and empty dots are repesenting the data set from Brazil. The relationship over entire data set can be expressed as *daily Js = 6.5 x max Js* (R^2 = 0.863, p < 0.0001).

put from the thermal dissipation probes was measured exactly the same way and 15 min averages were stored on data loggers (various models from the CR serious, Campbell Scientific Inc., Logan, UT, USA). Xylem sap flux densities were calculated using the standard Granier equation (Granier, 1987), given as

$$J_s = 0.0119 \times K^{1.231}$$

where K is the temperature differences between the heated probe and the reference probe for no flux and positive xylem flux. Daily maximum sap flux is defined as the maximum value (15 min values) recorded on a given day. The absolute maximum xylem sap flux densities was reached with 60 g cm^{-2} h^{-1} and measured in the plantations in Panama (compare Fig. 1). The maximum xylem sap flux densities in the Brazilian Amazon reached in the values up to 24 g cm^{-2} h^{-1} (compare Fig. 1). The lower maximum values in the Amazon are mainly explained by the much lower vapor pressure deficit compared to the more seasonal climate in Panama (Kunert et al., 2015a), however the recorded values are in line the range of maximum values reported in the literature. Studies reviewing a variety of tropical xylem sap flux studies and give a range of maximum xylem sap flux densities between 5 and 70 g cm^{-2} h^{-1} (Dierick et al., 2010; Horna et al., 2011). Daily xylem sap flux densities recoded in Panama were up to 500 g cm^{-2} h^{-1}, whereas only 250 g cm^{-2} h^{-1} was measured in the Brazilian Amazon. Maximum xylem sap flux values and daily xylem sap flux values were highly significant linearly related (Fig. 1, R^2 = 0.863, p < 0.0001). This linear relationship with a slope of 6.5 applied across all 48 investigated species, all study sites and the variety of forest systems studied. This relationship also applied on species level across the different tree individuals and across species with different species traits (Fig. 2), and even across plant groups with large differences in their hydraulic conduit properties (Aparecido et al., 2015). The linear relationship is described as: *daily* J_s = *6.5 x max* J_s (Fig. 3). To my knowledge, this is a new aspect of xylem sap flux and the geometry of the diurnal xylem sap flux course with its maximum has not yet been discussed in the literature. A more geometric explanation for the strong correlation might come from bell-shaped characteristic of diurnal sap flux courses (Johnson et al., 2011; Lu et al., 2000, 2002), however the connection of this relationship between daily and maximum xylem sap flux has not yet been drawn in this context. Definitively, the pattern of diurnal xylem sap flux course has some similarity with a relatively symmetrically shaped bell curve on days when maximum values are measured at noon or similarity with a skewed bell curve when maximum values are recorded a

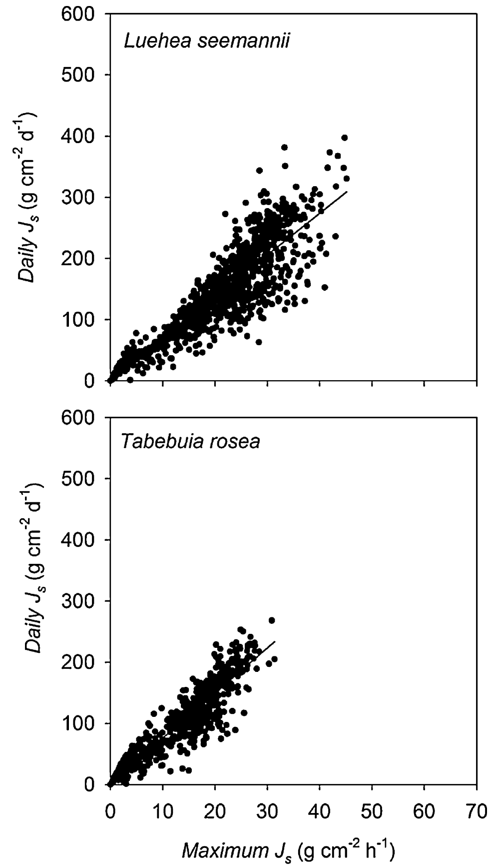

Fig. 2. Liner relationship between daily xylem sap flux and maximum xylem sap flux of *Luehea seemannii* (n = 12 trees, R^2 = 0.803, p < 0.0001) and *Tabebuia rosea* trees (n = 12 trees, R^2 = 0.920, p < 0.0001) differing in their relative growth rates (Scherer-Lorenzen et al., 2005) and their leaf traits (Schneebeli et al., 2011), but both having the same slope of 6.5 between daily xylem sap flux and maximum xylem sap flux. Both species were growing on an experimental tree planataion in Panama (Kunert et al., 2012).

little bit before or after noon. The timely distribution of the curve stays constant all year round as the tropics are characterized by almost equal day length or low variation in day length throughout the year. Day length e.g. in Manaus is 12 h with only 21 min difference between longest day and the shortest day of the year. The root of the bell shaped function is constant throughout the year and always at the same time in morning with sunrise. The maximum is reached about six hours later around noon and represents the stationary point or abscissa of the bell curve. The most important variable influencing the daily xylem values is the maximum xylem sap flux what is the abscissa of the maximum of a bell curve and dependent on environmental factors as explained above. The water that moved upwards until reaching the abscissa needs to be refilled by the same amount, even if it takes more than six hours to refill the amount of water and xylem sap flux extends accordingly into the night. Hence, the bell shape of diurnal xylem flux must not be symmetrical and can have an asymmetrical right skewed shape. This simplifying relationship between daily and maximum xylem sap flux values is of great value for modeling approaches as it reduces the number of estimates to a minimum number of variables. A possible explanation of this geometric relationship could be the inertia of the water transport systems. This means that xylem sap flux has a resistance to any change in its state of motion which includes changes to its velocity or the state of rest. Such inertia of xylem sap flux has been described in various ways. The response of xylem sap flux to vapor pressures deficit (VPD) is for example characterized by a hysteresis and representing a delay in canopy