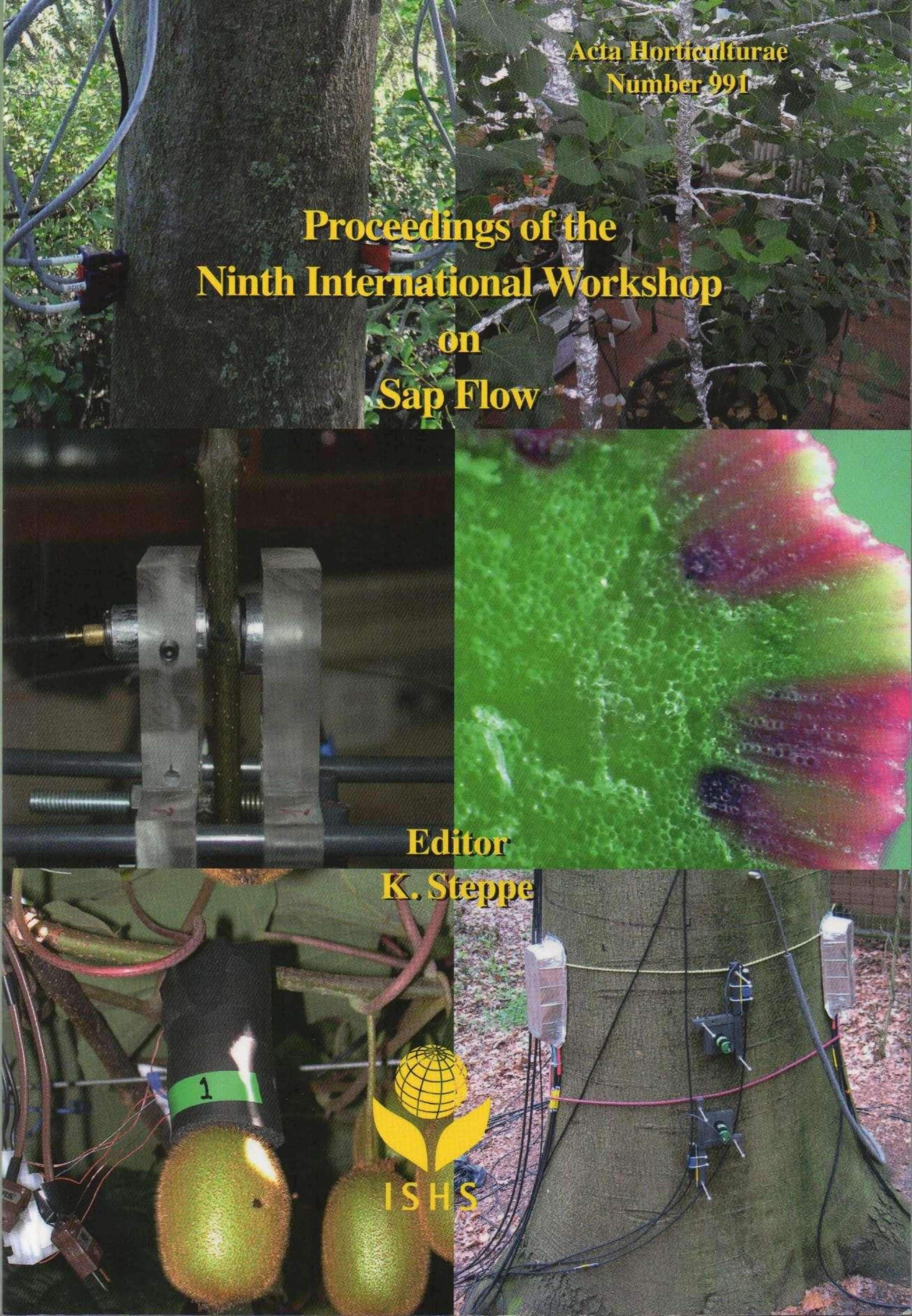

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K. Steppe

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Water Storage Discharge and Refilling in the Main Stems of Canopy Tree Species Investigated Using Frequency Domain Reflectometry and Electronic Point Dendrometers

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Keywords: Fourier time series, sapwood capacitance, subtropical trees, volumetric water content, water transport

Abstract

Water storage in the trunks of large trees plays an important role in whole-plant water balance on both daily and seasonal bases. To investigate the dynamics of water storage and usage in tree trunks, diurnal changes in volumetric water content (VWC) of the sapwood and tree radius including the bark were monitored continuously using frequency domain moisture sensors and electronic point dendrometers in 10 canopy tree species of a subtropical seasonal forest in northern Argentina. In addition, species-specific water storage capacitance of the active xylem was assessed using pressure volume relationships determined with a psychometric method. In nearly all the species, trunk VWC and radius length decreased during the day when the air saturation deficit increased, suggesting that the trunk water storage was drawn by canopy transpiration, while the increase of VWC during the night suggests stem water storage recharge. Species with higher water storage capacitance exhibited lower wood density and higher average VWC, suggesting the influence of wood structural properties on its water storage function.

INTRODUCTION

Moisture sensors based on frequency domain reflectrometry (FDR) have been widely used for measurements of soil water content (Czarnomski et al., 2005), however they have only recently been successfully used to monitoring the water status of living trees (Hao et al., 2013). Holbrook et al. (1992) used sensors based on the same principle to monitor relative changes in volumetric water content in stems of palm trees. However, because the temperature induced changes in apparent dielectric content of palm stems exceeded the temperature dependence of the dielectric content of water, absolute values of volumetric water content was not determined. The FDR moisture sensor used in the present study has high precision, high temporal resolution, low temperature sensitivity and a convenient installation configuration, and is therefore an ideal tool for measuring stem volumetric water content (VWC) in trunks accurately and continuously. The in situ measurements of trunk wood water status using the non-destructive method allow us to study in detail a series of important questions regarding plant water relations, such as the role of trunk water storage in short-term (diurnal) and long-term (seasonal) water balances (Hao et al., 2013).

The tree trunk, with both long distance water transport and storage functions, plays an important role in whole-plant water relations (Holbrook, 1995; Goldstein et al., 1998; James et al., 2003; Scholz et al., 2007; Steppe et al., 2012). However, due to technical difficulties, most studies on tree hydraulic architecture are limited to peripheral organs, such as roots, terminal branches and leaves, although in the last decade there were

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some investigations in trunk water relations using electronic dendrometers and sap flow techniques (e.g., Zweifel et al., 2000; Scholz et al., 2007; Steppe et al., 2012). The objective of this study was to evaluate the dynamics of water storage discharge and refilling in the trunk of canopy trees in a subtropical seasonal forest in northern Argentina. To carry out this investigation, VWC, and stem radius fluctuations were measured continuously during several months in evergreen and deciduous tree species. Furthermore, sapwood capacitance, wood density and environmental conditions were measured to assess factors influencing the water storage functions of tree trunks.

MATERIALS AND METHODS

The research was conducted in the Iguazú National Park (INP; 25°31'-25°43'S, 54°08'-54°32'O) in northern Argentina. Mean annual precipitation in the area is about 2000 mm, evenly distributed throughout the year. Mean annual air temperature is 21°C with monthly means of 25°C in January and 15°C in July. The study site is a typical native subtropical seasonal forest in this region. The forest has mature canopy trees ranging from 20 to 45 m in height with abundant lianas and epiphytes. The canopy is mostly dominated by trees of the genera *Cordia* (*Boraginaceae*), *Ocotea* and *Nectandra* (*Lauraceae*), *Parapiptadenia* and *Peltophorum* (*Fabaceae*), *Cedrela* and *Trichilia* (*Meliaceae*) and *Plinia*, *Eugenia* and *Myrciaria* (*Myrtaceae*). For the present study 10 species were studied.

Moisture sensors based on frequency domain reflectometry (FDR) technology (Model GS3, Decagon Devices, Inc. Pullman, WA) were installed in the main stem sapwood at breast height. Details of sensor installation and calibration are described by Hao et al. (2013). Briefly, the three metal prongs (5.5 cm in length, 3.26 mm in diameter, and 2.54 cm apart) of the GS3 sensor were inserted into fresh drilled holes (3.26 in diameter) in the sapwood of the trunks (bark under the sensor overmould was removed). A small section of the trunk including the sensor was wrapped with foam to allow the sensor and the sapwood remains in thermal equilibrium. Data were recorded using EM50 data loggers (Decagon Devices, Inc. Pullman, WA) every 10 min. Trunk radius was continuously monitored with point electronic dendrometers with very low temperature sensitivity (0.27 μm $°C^{-1}$) (ZN11-T-WP; Zweifel Consulting, Hombrechtikon, Switzerland). The electronic displacement-sensor (linear motion potentiometer) was in contact with the bark (only a small portion of dead bark was shaved) and consequently diurnal radius variations reflected changes in water content in the xylem and active bark tissues. In one experiment, the displacement sensor was in contact with the xylem surface (through a small drill hole in the bark). A pressure-volume technique was used to estimate sapwood capacitance (Scholz et al., 2007). Environmental data were obtained from a meteorological station located 500 m from the study site at approximately the same elevation.

We analyzed the variations in VWC and trunk radius through Single Spectrum (Fourier) Analysis. Unless otherwise indicated, variations in stem radii represent dimensional changes due to variations in water content of both xylem (sapwood) and live cells in the bark. Spectrum analysis is a powerful tool in the interpretation of cyclical patterns of time related trends, which allows a complex time series with cyclical components to be decomposed into a small number of underlying sine and cosine functions of particular wavelengths. Using Fourier analysis it is possible to uncover a few recurring cycles of different time lengths in the time series (Wei, 1989). If there is strong periodicity in a given time period, a large correlation (sine or cosine coefficient) will be observed. The periodogram can be interpreted in terms of variance of the data at the respective period. The relationships between the different variables were explored by regression analysis and by fitting linear and exponential decay functions to the data.

RESULTS AND DISCUSSION

Stem radius and VWC increased substantially after rainfall events, for example around Julian days 155, 170, 187 and 208 (Fig. 1), which indicate increased water storage in both xylem and bark tissues. When water availability is high during these wet periods, water content in parenchyma tissues, fibers and living tissue of the bark will increase probably due to less negative water potentials. During a relatively long period without precipitation (Julian day 175 to Julian day 187), the air saturation deficit (ASD) increased continuously. During this period the trunk size, as measured by stem radius, decreased but the overall sapwood VWC remained more or less constant (Fig. 1). The diurnal variations in trunk radius during Julian day 175 to Julian day 187 were on average 80 μm. When diurnal variations in radius were obtained only in the xylem, the magnitude of the variation was much smaller, about 8 to 10 μm, which may be due to the relative inelasticity of xylem tissue compared to that of cortical cells.

The sapwood VWC and trunk radius of two species were plotted against time (Fig. 2) during a short period without precipitation and similar ASD. In both species, VWC of the sapwood and the stem radius decreased during the daytime when evaporative demand increased (ASD increases). The opposite pattern was observed at night: ASD dropped to very low values approaching 0 kPa while the VWC and the stem radius increased. Most of the species studied show similar patterns of VWC and radius variations. The decrease in VWC diurnally suggests that stored water in the trunk is used by canopy transpiration during the daytime, while the increase of VWC during the night suggests trunk water storage recharge. The trunk radius showed obvious overall decrease during dry periods but VWC remained relatively constant, as shown in the examples of *B. ridelianum* and similar in *C. gonocarpum* (Fig. 2). Figure 3 shows that the 24 h period explains a large percentage of the variance for VWC and that 96 h (the entire sampling period of 4 days), explain a larger percentage of the variance for stem radius change, particularly for *B. riedelianum*. A plausible explanation of the pattern which occurs during periods with no precipitation is that a relatively large amount of water is provided by the living cells of the bark, resulting in a stem size decrease over time, and that nighttime recharge is incomplete for the bark, consistent with the drying of the soil and the water storage becoming into equilibrium with the soil water status. On the other hand, the VWC oscillate around the same value or with a relatively weak trend, suggesting that sapwood water content tend to remain approximately constant with a strong VWC oscillation of a 24 h period. Preliminary results suggest that species studied in the current research project with very high sapwood capacitance and thick bark (e.g., *Ceiba speciosa*) has a very different diurnal pattern of VWC variations, increasing during the daytime when evaporative demand is relatively high and decreasing at nighttime. A potential explanation for the increase in VWC during the day could be a substantial decrease in xylem volume and/or a very large amount of water delivered to the sapwood by the living tissues in the bark. Additional studies will be done with heat dissipation methods for measuring sap flow, xylem and bark variations estimates with dendrometers, and VWC measurements done simultaneously in xylem and bark.

When water released from the sapwood was plotted as a function of water potentials, all species exhibited an initial phase in which cumulative water release increased in a nearly linear fashion as water potential, measured with psychrometers, declined to a threshold value (Fig. 4). After this threshold, water released by the sapwood increased slowly and asymptotically, although low water potentials beyond the threshold may not be experienced by the stem tissues under normal conditions (Zweifel et al., 2000). The slopes of the initial linear portions of the water released versus water potential were used as estimates of the species-specific capacitance values across the normal physiological operating range of tissue water potential. While water storage capacity measured by FDR is an extensive property, capacitance reflects the storage tissue potential ability to release water to the xylem in responses to water potential gradients (Scholz et al., 2011). Capacitance values in the 10 studied species ranged from 762 to 46 kg m^{-3} MPa^{-3} for *Ceiba speciosa* and *Lonchocarpus muehlbergianus*. Capacitance was functionally related to wood density by a negative exponential relationship across species with higher capacitance in species with lower wood density (Fig. 5a). Scholz et al. (2007) found a similar trend between capacitance and wood density for savanna tree species, however, the relationship across species in their study was linear. Sapwood capacitance, in our study, increased linearly with increasing average volumetric water content across species (Fig. 5b).

CONCLUSIONS

The diurnal patterns of VWC and stem radius variation, as well as their response to environmental factors, suggest that the bark and the active xylem tissues of the trunk are hydraulically well connected. Both active xylem and bark tissues contribute to the overall stem capacitance despite difference in the magnitude of the radius oscillations (larger in the bark and smaller in the xylem tissue). Water moves radially from the bark to the sapwood depending on the direction and magnitude of the water potential gradient. We hypothesize that during the daytime, tension increases in the xylem conduits due to leaf transpiration, lowering the water potential of all xylem cells resulting in a water potential gradient favorable for water movement from the bark to the sapwood, which decreases bark thickness due to cell shrinkage. When stomata close in the evening and tension in the xylem conduits decreases water moves radially in the opposite direction from xylem to bark. Phloem is one of the important living cell tissues in the bark that transport osmotically active solutes from the source in the leaves to the sink in other portions of the plants, which may contribute to the generation of a nighttime water potential gradient inducing water movement into the bark. Sevanto et al. (2011) hypothesized that changes in hydraulic conductance or/and changes in osmotic concentration in the phloem can also be involved in the rate and direction of radial water exchange. The prerequisite for this radial water exchange in the stem of the plants is an adequate hydraulic connection between xylem and bark tissues. Steppe et al. (2012) suggested that radial hydraulic conductance across bark and xylem tissues in stems might be variable and possibly facilitated by aquaporins.

ACKNOWLEDGEMENTS

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Literature Cited

Czarnomski, N.M., Moore, G.W., Pypker, T.G., Licata, J. and Bond, B. 2005. Precision and accuracy of three alternative instruments for measuring soil water content in two forest soils of the Pacific Northwest. Can. J. For. Res. 35:1867-1876.

Goldstein, G., Andrade, J.L., Meinzer, F.C., Holbrook, N.M., Cavalier, J., Jackson, P. and Celis, A. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ. 21:397-406.

Hao G.-Y., Wheeler, J.K., Holbrook, N.M. and Goldstein, G. 2013. Investigating xylem embolism formation, refilling and water storage in tree trunks using frequency domain reflectometry. J. Exp. Bot. (in press).

Holbrook, N.M., Burns, M.J. and Sinclair, T.R. 1992. Frequency and time-domain dielectric measurements of stem water content in the arborescent palm *Sabal palmetto*. J. Exp. Bot. 43:111-119.

Holbrook, N.M. 1995. Stem water storage. p.151-174. In: B.L. Gartner (eds.), Stem and Trunks in Plant form and Function. Academic Press, San Diego.

James, S.A., Meinzer, F.C., Goldstein, G., Woodruff, D., Jones, T., Restom, T., Mejia, M., Clearwater, M. and Campanello, P. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. Oecol. 134:37-45.

Sevanto, S., Holtta, T. and Holbrook, N.M. 2011. Effects of the hydraulic coupling between xylem and phloem on diurnal phloem diameter variation. Plant Cell Environ. 34:690-703.

Scholz, G.S, Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C. and Miralles-Wilhelm, F. 2007. Biophysical properties and functional significance of stem waterstoragetissues in Neotropical savanna trees. Plant Cell Environ. 30:236-248.

Scholz, G.S., Phillips, N.G., Bucci, S.J., Meinzer, F.C. and Goldstein, G. 2011. Hydraulic capacitance; biophysic and functional significance of internal water sources in relation to tree size. p.341-361. In: F.C Meinzer et al. (eds.), Size- and Age-Related Changes in Tree Structure. Springer, New York.

Steppe, K., Cochard, H., Lacointe, A. and Améglio, T. 2012. Could rapid diameter changes be facilitated by a variable hydraulic conductance? Plant Cell Environ. 35:150-157.

Wei, W.W. 1989. Time series analysis: univariate and multivariate methods. Addison-Wesley, New York.

Zweifel, R., Item, H. and Häsler, R. 2000. Stem radium changes and their relation to stored water in stems of young Norway spruce trees. Trees 15:50-57.

Figures

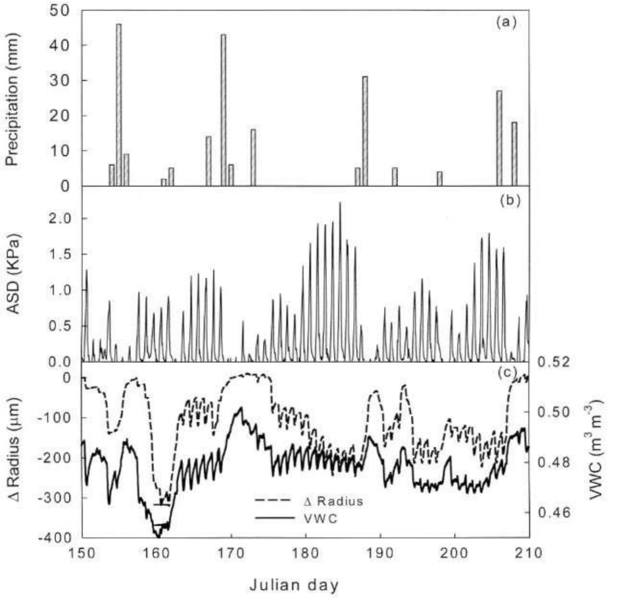

Fig. 1. Long term dynamics of (a) precipitation, (b) Air saturation Deficit (ASD) and (c) variation in stem size normalized by initial radius (Δ Radius) and Volumetric water content (VWC) in the main stem of a *Chrysophyllum gonocarpum* canopy tree.

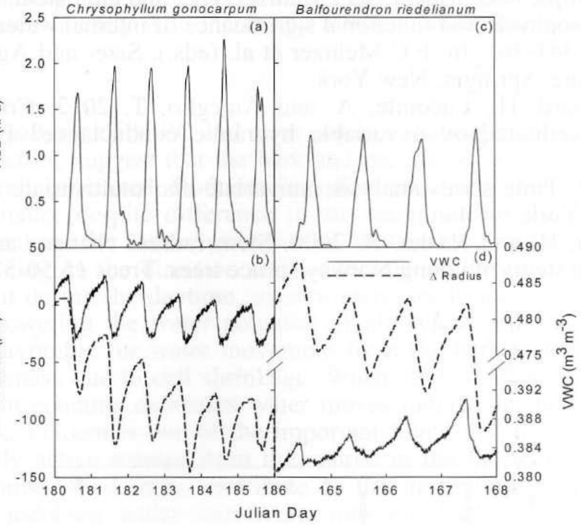

Fig. 2. Diurnal variation in air saturation deficit (ASD; a, c), stem size variation normalized by the initial radius (Δ radius, dashed line) and volumetric water content (VWC; solid line) in the main stem of *Chrysophyllum gonocarpum* (b) and in the main stem of *Balfourendron riedelianum* (d). Measurements of ASD were obtained every hour and Δ Radius and VWC every 10 minutes.

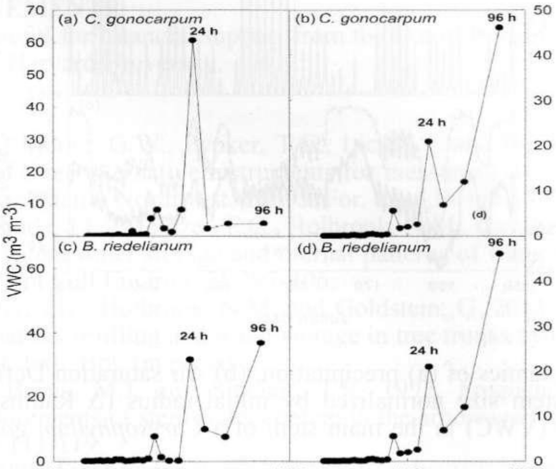

Fig. 3. Single Spectrum Fourier analysis of volumetric water content (VWC; a, c) and stem size (Δ Radius, b, d) of *Chrysophyllum gonocarpum* and *Balfourendron riedelianum* showing the variance of several time periods (the inverse of frequency: cycles per unit of time) of data from Figure 2. High variance indicates strong periodicity in the variable measured (either VWC or stem radius) in a given time period. The two most important periods (the time in which a cycle is being completed in the series) are 24 and 96 h and are indicated in the figure. The scale of the x-axis was $\log_{10}$ transformed.

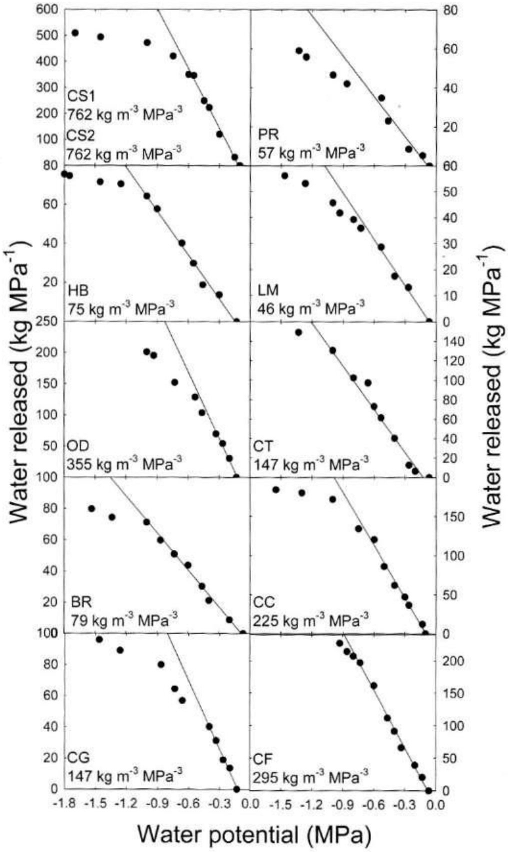

Fig. 4. Water released as a function of stem water potential for 10 dominant canopy species in the study area. The values of capacitance are indicated in each panel. The species symbols are: Cs (*Ceiba speciosa*), Pr (*Parapiptademia rigisa*), Hb (*Holocalyx balansae*), Lm (*Lonchocarpus muehlbergianus*), Od (*Ocotea diospirifolia*), Ct (*Cordia trichotoma*), Br (*Balfourodendron riedelianum*), Cc (*Cabralea canjerana*), Cg (*Chrysophyllum gonocarpum*) and Cf (*Cedrella fisssilis*). Note the differences in y-axes scales for each species.

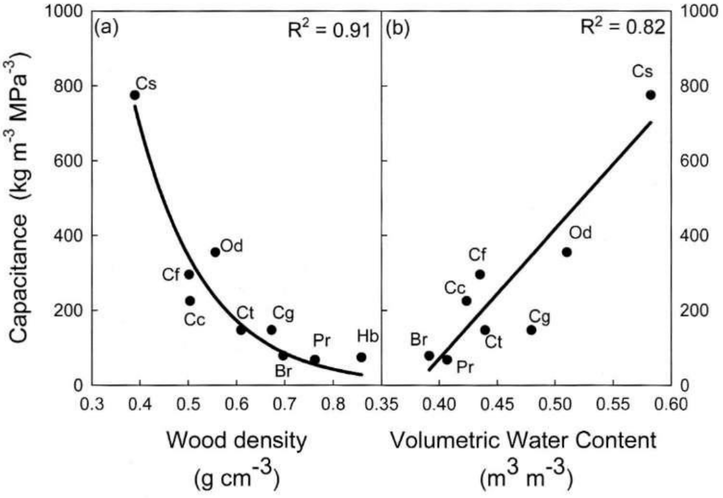

Fig. 5. Functional relationship for several canopy species between sapwood capacitance and sapwood density (a), and between sapwood capacitance and volumetric water content (information on VWC in Hb species was not obtained, b). Symbols of the species are in legend of Fig. 4. For data in panel (a) an exponential decay function was fitted ($y=11251\ e^{-7x}$) and for (b) a linear regression was used ($y=3460x - 1313$).