

Stem diameter variation: endogenous regulation versus environmental dynamics and its implication for functional modelling

Maurits Vandegheuchte¹, Adrien Guyot², David Lockington² and Kathy Steppe¹

¹Laboratory of Plant Ecology, Faculty of Bioscience Engineering, Ghent University, Coupure links 653, 9000 Gent, Belgium, ²National Centre for Groundwater Research and Training- School of Civil Engineering, The University of Queensland, 4072 Brisbane, Australia

*correspondence: maurits.vandegheuchte@ugent.be

Highlights: Stem diameter variations are generally modelled based on the time lag between transpiration and root water uptake. However, small differences in endogenous osmotic regulation of the storage tissue can result in significant changes in stem diameter variation. This endogenous control needs to be taken into account in functional-structural plant models to accurately predict growth.

Keywords: stem diameter variation, *Rhizophora*, *Avicennia*, growth, osmotic regulation

INTRODUCTION

When interpreting and modelling the plant water status, radial transport between xylem and surrounding storage tissues is of crucial importance as it allows turgor to build up which ultimately leads to plastic growth, providing a specific threshold pressure is overcome (Lockhart, 1965). Moreover, water in the storage tissue buffers discrepancies between water demand and supply, avoiding hydraulic failure in the xylem. As such, it has been commonly accepted that a clear time lag exists between the transpiration at leaf level and the water uptake at root level, caused by the hydraulic resistance between the two (e.g. Zweifel et al., 2000, Peramaki et al., 2001, Sevanto et al., 2002, Steppe et al., 2006). This time lag causes a decrease in stem diameter in the morning as then the water supply from the roots lags behind the transpiration at leaf level, necessitating water flow from the storage compartments (Hinckley and Bruckerhoff, 1975). In the afternoon, when xylem water potential rises because of a decreased atmospheric water demand, water again flows back to the storage tissues, resulting in a diameter increase (Molz and Klepper, 1973).

In functional plant models, diameter changes are modelled based on the in- and outflow of water in the storage tissues from and to the xylem. In these models, the single cell approach is often applied, considering the stem storage as a single volume separated from the xylem by a water permeable membrane with a specific resistance (e.g. Génard et al., 2001, Steppe et al., 2006). Water transport to this storage compartment then increases turgor, resulting in dynamic diameter changes or plastic growth if a threshold value is exceeded. In these models, however, endogenous osmotic activity is not taken into account.

Our aim was to assess possible differences in diameter variations and coupled endogenous osmotic regulation between two representatives of the two most dominant mangrove genera, *Avicennia marina* (Forssk.) Vierh. and *Rhizophora stylosa* Griff. These species are known to thrive in saline, and, hence, drought inducing conditions, requiring specific water use strategies.

MATERIALS AND METHODS

Measurements were conducted at the west coast of North Stradbroke Island, Queensland, Australia (S27°27.061' E135°25.806'), a vegetated sand dune island. The island is characterized by sandy soils and acidic waterbodies intertwined by a complex mix of groundwater-fed lakes, swamps and creeks (Page *et al.*, 2012). On this field site, three full grown trees of both *Avicennia marina* (Forssk.) Vierh. and *Rhizophora stylosa* Griff. were chosen, located in proximity of each other to avoid tidal effects and spatial salinity gradients. The field site was subjected to tidal movement, flooding the site approximately twice every 24 hours. Air temperature, relative humidity, solar radiation, rainfall and windspeed were measured and recorded every ten minutes at 2 m above soil surface (HOBO weather station, Onset, Cape Cod, Massachusetts, USA). Vapour pressure deficit (*VPD*, kPa) was inferred from measured air temperature (T_{air}) and relative humidity (*RH*) according to Buck (1981). Soil salinity and water table depth were determined with in situ pressure sensors (Aqua Troll 200, In-Situ Inc., Fort Collins, CO, USA) installed in piezometers, located close to the measured trees at depths of 25 and 180 cm. All trees were equipped with a dendroband

(DRL26 – Logging Band Dendrometer, ICT international, Armidale, NSW, Australia), continuously recording stem diameter variations, and Sapflow+ sensors, registering sap flux density (Vandegehuchte and Steppe, 2012). Stem water potentials were recorded with stem psychrometers (PSY-1 Stem Psychrometer, ICT International, Armidale, NSW, Australia). Besides these continuous measurements, stomatal resistance was measured for four days (DOY 241, 247, 251 and 254) throughout the measurement period, applying a dynamic porometer (AP4 dynamic porometer, Delta-T Devices Ltd, Cambridge, UK).

By slightly modifying the mathematical flow and storage model of Steppe et al. (2006) based on the work of De Swaef et al. (2012), a mechanistic model was obtained to assess dynamics in xylem and storage water potentials based on stem sap flux density and stem diameter variations. This model was applied as a tool to synthesise the conducted measurements and derive trends in osmotic potential of the stem storage tissue. Modelled xylem water potentials were compared with psychrometric measurements.

RESULTS AND DISCUSSION

Contrary to what is expected from literature, stem diameter of *Rhizophora* increased during the morning and decreased in the afternoon. Even though a similar pattern has been shown for CAM plants (Gouws et al., 2005, Matimati et al., 2012), stomatal closure was measured during the night, indicating that the CAM mechanism was not applicable for *Rhizophora*. As sap flux density and stem water potential showed similar patterns for *Avicennia* and *Rhizophora* and these trees were subjected to the same environmental conditions, the differences in diameter variations patterns are likely due to endogenous osmotic regulation. Our model outputs based on stem diameter input suggest that, unlike what is generally expected, xylem water potential lags behind the storage water potential for *Rhizophora* (Figure 1b), due to an earlier decline in storage osmotic potential compared to *Avicennia* (Figure 2a). When decoupling the volumetric effect and the presence of osmotic active compounds on storage osmotic water potential, it is clear that, while both species seem to endogenously regulate the amount of osmotic compounds present in the storage tissues, *Rhizophora* manages to increase this amount earlier during the day than *Avicennia* (Figure 2b).

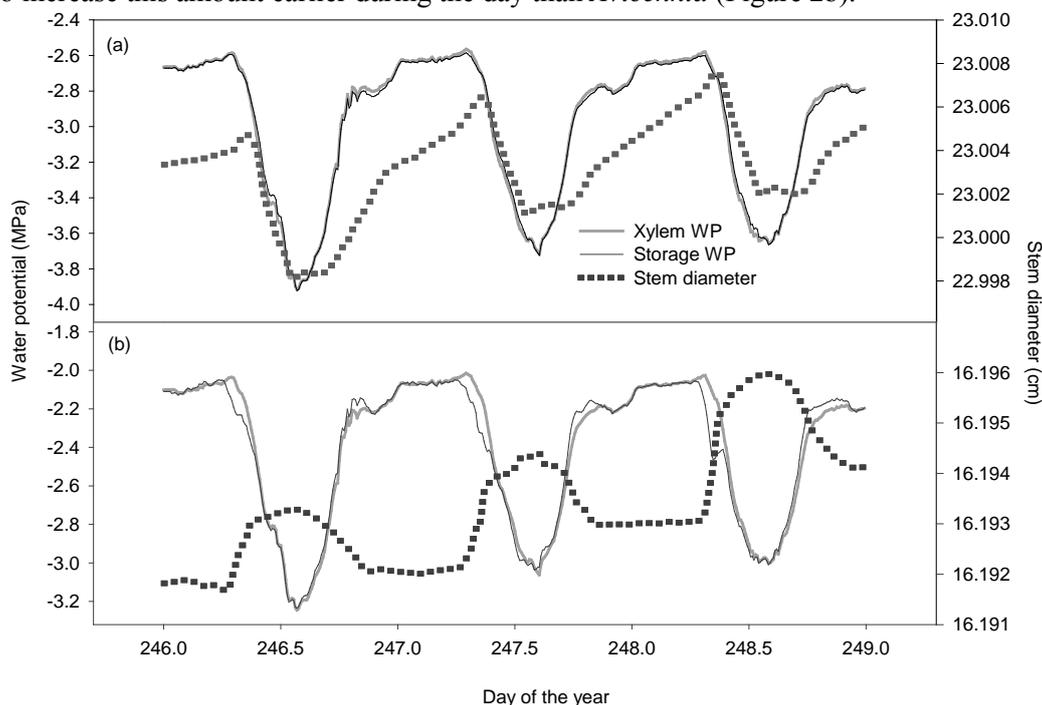


Figure 1 Model results showing the diameter input and xylem and storage water potential output for both *Avicennia* (a) and *Rhizophora* (b).

These results indicate that stem diameter variations, and, hence, growth, may not only be determined by environmental dynamics but may also be strongly influenced by endogenous control. This implies that also these endogenous adaptations need to be included in functional-structural plant models to allow correct predictions of plant behaviour. Our results indeed show that very small differences in osmotic active compound regulation may have drastic influences on important plant physiological variables such as stem diameter. A more thorough knowledge on how these features influence stem diameter variations will result

in new insights into why species differ in growth patterns and, hence, which strategies are more beneficial, depending on the environmental conditions. Moreover, it will allow to assess the relative importance of endogenous regulation and environmental dynamics to long-term growth.

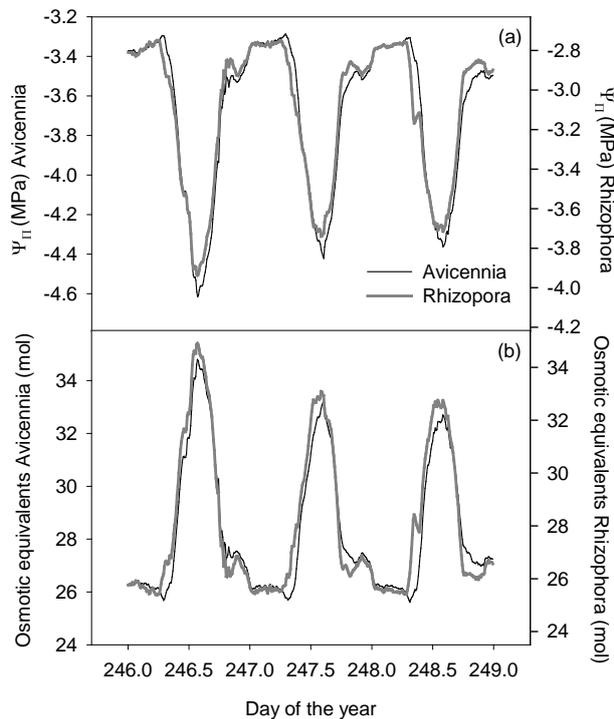


Figure 2 Osmotic potential of the storage tissue (a) and derived osmotic equivalents of the entire storage volume (b) for *Avicennia* and *Rhizophora*

LITERATURE CITED

- Buck AL. 1981.** New Equations for Computing Vapor Pressure and Enhancement Factor. *Journal of Applied Meteorology*, **20**: 1527-1532.
- De Swaef T, Hanssens J, Cornelis A, Steppe K. 2012.** Non-destructive estimation of root pressure using sap flow, stem diameter measurements and mechanistic modelling. *Annals of Botany*.
- Génard M, Fishman S, Vercambre G, Huguet JG, Bussi C, Besset J, Habib R. 2001.** A biophysical analysis of stem and root diameter variations in woody plants. *Plant Physiology*, **126**: 188-202.
- Gouws LM, Osmond CB, Schurr U, Walter A. 2005.** Distinctive diel growth cycles in leaves and cladodes of CAM plants: differences from C(3) plants and putative interactions with substrate availability, turgor and cytoplasmic pH. *Functional Plant Biology*, **32**: 421-428.
- Hinckley TM, Bruckerhoff DN. 1975.** The effects of drought on water relations and stem shrinkage of *Quercus alba*. *Canadian Journal of Botany*, **53**: 62-72.
- Lockhart JA. 1965.** An analysis of irreversible plant cell elongation. *Journal of Theoretical Biology*, **8**: 264-275.
- Matimati I, Musil CF, Raitt L, February EC. 2012.** Diurnal stem diameter variations show CAM and C-3 photosynthetic modes and CAM-C-3 switches in arid South African succulent shrubs. *Agricultural and Forest Meteorology*, **161**: 72-79.
- Molz FJ, Klepper B. 1973.** On the Mechanism of Water-Stress-Induced Stem Deformation1. *Agronomy Journal*, **65**: 304-306.
- Page TJ, Marshall JC, Hughes JM. 2012.** The world in a grain of sand: evolutionarily relevant, small-scale freshwater bioregions on subtropical dune islands. *Freshwater Biology*, **57**: 612-627.
- Peramaki M, Nikinmaa E, Sevanto S, Iivesniemi H, Siivola E, Hari P, Vesala T. 2001.** Tree stem diameter variations and transpiration in Scots pine: an analysis using a dynamic sap flow model. *Tree Physiology*, **21**: 889-897.
- Sevanto S, Vesala T, Peramaki M, Nikinmaa E. 2002.** Time lags for xylem and stem diameter variations in a Scots pine tree. *Plant Cell and Environment*, **25**: 1071-1077.
- Steppe K, De Pauw DJW, Lemeur R, Vanrolleghem PA. 2006.** A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. *Tree Physiology*, **26**: 257-273.
- Vandegheuchte MW, Steppe K. 2012.** Sapflow+: a four-needle heat-pulse sap flow sensor enabling nonempirical sap flux density and water content measurements. *New Phytologist*, **196**: 306-317.
- Zweifel R, Item H, Hasler R. 2000.** Stem radius changes and their relation to stored water in stems of young Norway spruce trees. *Trees-Structure and Function*, **15**: 50-57.