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Long-term versus daily stem diameter variation in co-occurring mangrove species: Environmental versus ecophysiological drivers

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ABSTRACT

High temporal resolution stem diameter variation (SDV) patterns have been widely recognized as a tool to study fundamental plant physiological mechanisms underlying whole-plant functioning and growth. As an integrative response to hydraulic and carbon related processes, SDV research has greatly improved insights in plant functioning of several herbaceous and woody species. Nevertheless, to date little detailed information on SDV and related physiological processes is available for mangrove species. By measuring continuous tree physiological variables such as stem diameter variations, sap flow and stem water potential in relation to the microclimatic conditions, the water use strategies of two co-occurring mangrove species, *Avicennia marina* (Forssk.) Vierh. and *Rhizophora stylosa* Griff. were investigated. Even though both species showed a similar long-term growth trend, closely linked to the environmental conditions, their daily SDV pattern was markedly different. While for *Avicennia marina* the SDV showed the standard daily pattern of morning decline and evening rise, the opposite daily SDV pattern was observed for *Rhizophora stylosa*. The contrasting patterns of SDV in both species thriving in the same environment indicates the importance and complexity of physiological endogenous mechanisms in addition to environmental conditions in controlling SDV and radial stem growth.

1. Introduction

Water flow in trees is generally explained by the cohesion-tension theory, stating that the evaporation of water from leaf cell walls, termed transpiration, causes tension in the xylem conduits, pulling water upwards through the soil-plant-atmosphere continuum (Angeles et al., 2004; Tyree and Zimmerman, 2002). However, at the onset of transpiration, when water evaporates and diffuses through the stomatal opening into the atmosphere, the water supply at root level does not yet meet the atmospheric demand because of the hydraulic resistance throughout the tree. This causes the xylem water potential to decrease, influencing the water potential gradient between xylem and storage tissues, which has a direct effect on the radial water flow between these tissues. As such, water within the storage tissues can minimize the temporal imbalances in water supply and demand. When transpiration diminishes in the afternoon and the xylem water potential increases again, these internal reserves can be replenished if the altered water potential gradient allows water flow into the storage tissues. As depletion and refilling influence the volume of the stem storage tissues, these daily dynamics in water storage can be revealed by monitoring the stem diameter variation (SDV) (Goldstein et al., 1998; Peramaki et al., 2001; Sevanto et al., 2002; Steppe and Lemeur, 2004; Zweifel et al., 2000; Zweifel et al., 2001).

As the radial water flow results from a water potential gradient between xylem and storage tissues, daily SDV are also highly influenced by carbon-related processes such as leaf and woody tissue photosynthesis, phloem loading and unloading, local compartmentalization and production of osmolytes, and respiration (Daudet et al., 2005; De Schepper and Steppe, 2010; Hölttä et al., 2006; Schmitz et al., 2012; Sevanto et al., 2003). However, the effects of plant carbon status on SDV are considered to be somewhat less immediate in comparison to plant water status as plants seem to

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maintain a rather steady carbon supply to the sinks (De Swaef et al., 2013a).

Besides daily SDV, the interaction between hydraulic and carbon-related processes also determines long-term SDV trends including irreversible stem diameter growth. This irreversible growth requires sufficient water transport to allow the internal cell turgor pressure to exceed a certain threshold value, causing cell expansion on the one hand and the structural incorporation of carbohydrates into the cell on the other hand (Daudet et al., 2005; Génard et al., 2001; Lockhart, 1965; Steppe et al., 2006). When these prerequisites are not met, structural growth cannot occur and stem diameters may show a decreasing trend, indicating an unfavourable water and/or carbon balance. As such, SDV patterns have been widely applied in irrigation studies and applications (Fernandez and Cuevas, 2010; Ortuno et al., 2010), and as a means to evaluate drought stress on plant functioning (Betsch et al., 2011; De Swaef and Steppe, 2010; Steppe et al., 2006; Zweifel and Hasler, 2001; Zweifel et al., 2005; Zweifel et al., 2006).

As high temporal resolution SDV measurements have played an important role in ecophysiological research, whether to determine the amount of stored water in trees, as a variable in water and sugar transport models or as an indication of ecosystem productivity (De Schepper and Steppe, 2010; De Swaef et al., 2013a,b; Hölttä et al., 2006; Sevanto et al., 2008; Steppe et al., 2006; Zweifel et al., 2010), their integrative value elucidating both water and carbon processes has been little exploited in studies of mangrove species. While growth of mangrove species has been assessed based on dendrochronological or low resolution stem diameter growth measurements (Day et al., 1996; Enoki et al., 2009; Estrada et al., 2008; Krauss et al., 2007; Liao et al., 2004; Nazim et al., 2013; Robert et al., 2011; Santini et al., 2012; Schmitz et al., 2008; Verheyden et al., 2004), it is surprising that, given the importance of mangal ecosystems (Alongi, 2008; Duke et al., 2007; Valiela et al., 2001), little attention has been paid to daily SDV patterns of mangrove trees resulting from high temporal resolution measurements so far.

In this study, stem diameter variations of two co-occurring mangrove species, *Avicennia marina* (Forssk.) Vierh. and *Rhizophora stylosa* Griff., were monitored at high temporal resolution and related to sap flow, stem water potential, stomatal resistance and microclimatic conditions during the dry winter season. We hypothesized that for both co-occurring species, notwithstanding a possible shift in time lag caused by species-specific biophysical processes, the stem diameters would respond largely similarly to the prevailing environmental conditions at the study site.

2. Materials and methods

Measurements were conducted at the west coast of North Stradbroke Island, Queensland, Australia (S27°27.061′ E135°25.806′, Fig. 1A) during the dry winter season (DOY 222 till 262) of 2012 as dry and mild climatic conditions prevail at this time of year and thus any confounding effects of rainfall could be excluded from the study. Focussing on measurements in the dry season made the potential influence of drought and the corresponding ecophysiological responses of the mangrove species to drought could be investigated.

This vegetated coastal sand island is characterized by a sandy soil and acidic water bodies that comprise a complex mix of perched groundwater-fed freshwater lakes, swamps and creeks (Page et al., 2012). The selected field site was co-dominated by *Rhizophora stylosa* Griff. and *Avicennia marina* (Forssk.) Vierh. At this field site, three full grown, representative trees of both *Avicennia marina* (Forssk.) Vierh., with an approximated average height of 5 m, and *Rhizophora stylosa* Griff., with an approximated average height of 3.5 m,were chosen. These trees were selected in close proximity

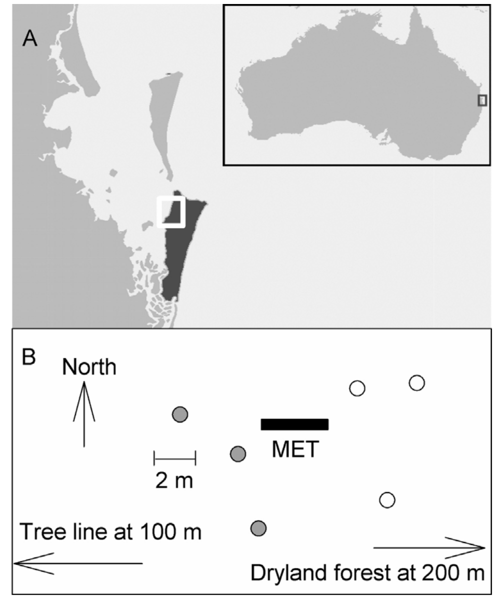

Fig. 1. (A) Location of the field site at the west coast of North Stradbroke Island, Queensland, Australia; (B) schematic of the measured trees at the mangrove field site. Filled circles are focal individuals of *Rhizophora stylosa* and open circles *Avicennia marina*.

to each other to minimize variation in tidal inundation and salinity (Fig. 1B, Table 1). The field site was subjected to regular tidal inundation with flooding of the site once to twice every 24 h. Air temperature, relative humidity, shortwave solar radiation, and wind speed were measured on-site every minute and averages recorded every ten minutes at 2 m above soil surface (HOBO weather station, Onset, Cape Cod, Massachusetts, USA). To ensure that shading effects of the weather station were negligible, a comparison with another weather station located in an open swamp 150 m from the mangrove site was conducted. Rainfall was measured using a tipping-bucket rain gauge. Vapor pressure deficit (VPD, kPa) was inferred from measured air temperature (T_{air}) and relative humidity (RH) according to Buck (1981).

Soil salinity, soil water conductivity and water table depth below ground level were measured every minute and averages recorded every 10 min from DOY 245 onwards with an in-situ pressure transducer (Aqua Troll 200, In-Situ Inc., Fort Collins, CO, USA) installed in a piezometer, located close to the measured trees at a depth of 0.25 m below the soil surface. Measurements of water table depth were corrected for external pressure fluctuations based on atmospheric pressure measurements at the site (Baro Troll 500, In-Situ Inc., Fort Collins, CO, USA). Actual measured soil water conductivity (AC in mS cm^{-1}) was converted to osmotic water potential Ψ_{Π} (MPa) based on McIntyre (1980):

$$\Psi_{\Pi} = -10^{1.091\log(AC)-1.46} \quad (1)$$

In 2013, one year after the experiments, pH, and redox potential were measured monthly *in situ* using a Hach Lange HQ40d portable pH, conductivity, and oxygen reduction potential multi-parameter meter (Hach Co. Loveland, CO, USA) from groundwater monitoring wells located adjacent to the study trees at depths of 1.5, 2.5, and 3.5 m below the sediment surface. All measurements occurred

Table 1
Tree stem diameter - Diameter at breast height (DBH) of the measured mangrove trees at the start of the measurement period.

Tree	Av1	Av2	Av3	Rhi1	Rhi2	Rhi3
DBH (m)	0.194	0.306	0.181	0.188	0.117	0.172