PLANT-WATER RELATIONS OF THE MANGROVE SPECIES RHIZOPHORA STYLOSA: A UNIQUE STORY

M. HUBEAU1, M.W. VANDEGEHUCHTE1, A. GUYOT2,3, C.E. LOVELOCK3,4, D.A. LOCKINGTON2,3, K. STEPPE1
1Laboratory of Plant Ecology, Faculty of Bioscience Engineering, Ghent University, Coupure links 653, 9000 Gent, Belgium
2National Centre for Groundwater Research and Training, Australia
3School of Civil Engineering, The University of Queensland, St. Lucia 4072, Australia
4School of Biological Sciences, The University of Queensland, St. Lucia 4072, Australia

INTRODUCTION

Water is an essential resource in trees for survival due to its involvement in a broad range of vital functions. For instance, water acts as a constituent, a solvent, a reactant and is responsible for the maintenance of cell turgidity (Kramer and Boyer 1995). As a consequence, trees have developed a wide variety of strategies to optimize their hydraulic architecture to cope with all sorts of prevalent conditions (Tyree and Ewers 1991).

Upward movement of water inside a tree is typically described by the cohesion-tension theory (Kramer and Boyer 1995). This theory states that the cohesion between water molecules is strong enough for a water column to move upward in xylem vessels without rupturing, even for pressures of several MPa. The suction force that moves water upward originates from transpiring leaves and due to cohesion water can be taken up by the roots.

When water is withdrawn from living cells the water potential inside these cells declines, which has serious implications on its functionality. Growth and cell wall synthesis but also photosynthesis are affected fairly rapidly by water shortage (Porporato et al. 2001).

Because of the implications of water shortage and drought stress, knowledge about the water status of trees provides valuable insights on the plant’s fitness and chances of survival. Stem diameter variation (SDV) is the result of several processes and dynamics inside the tree and hence comprises a lot of information. High time-resolution dendrometers can measure diel SDV patterns, which consist of a typical sequence and reflect the water status of the tree. Both reversible shrinkage and swelling and irreversible radial stem growth can be monitored. The former originates from short-term changes in water content, whereas the latter indicates irreversible changes in cell dimension (Steppe et al. 2006). The typical diel SDV pattern consists of three distinct phases, being the shrinkage phase, recovery phase and increment phase (Drew and Downes 2009). The shrinkage phase indicates a net loss of water inside the tree and takes place when water is transpired and internal water reserves are depleted. This phase takes place from morning until the afternoon. To compensate this water loss, water uptake in the roots occurs and when this water uptake becomes higher than the water loss, the recovery phase starts, typically in the afternoon (Drew and Downes 2009). At night, when water uptake continues, water reserves can be entirely replenished and growth becomes possible, meaning that the stem diameter increases compared to the previous day resulting in the increment phase.

Bad water household can result in net shrinkage instead of growth indicating a decline in water content and a state of stress (Deslauriers et al. 2007). This typical pattern has been consistently reported for C₃ plants (De Swaef et al. 2009, Drew and Downes 2009).

Because mangrove trees grow and thrive in a very challenging physiologically dry environment, this research was set up to unravel the adaptations and behavior developed by the mangrove species Rhizophora stylosa to survive. Mangrove trees are unique in the sense that they grow in the intertidal zone of tropical and subtropical seas and oceans, an area that is confronted with
recurrent flooding (Robert et al. 2009). The main challenges in these regularly flooded areas are anoxic conditions when flooded, high temperature, high irradiance and high levels of salinity (Medina 1999, Robert et al. 2009). Most trees are not able to withstand high salt concentrations and are damaged or even killed when confronted with elevated salinity (Allen et al. 1994). (True) mangroves on the contrary thrive under conditions of elevated salinity and cannot survive in the absence of a certain amount of salt (Medina 1999). Mangrove communities are not only fascinating because they can flourish despite these challenges, but at the same time they have a very important ecological function as they are important for terrestrial and marine food webs and act as both an atmospheric CO₂ sink and a carbon source for oceans (Duke et al. 2007). Economically, mangroves have a high value because they provide resources such as food, they generate income for fisheries and they offer protection against storms and sea-level rise (Duke et al. 2007). Nonetheless, mangrove areas are declining extremely rapidly at an alarming rate of 1 to 2% per year (Duke et al. 2007). This makes research on how mangroves survive in these harsh conditions relevant from both an ecophysiological and an ecological perspective.

MATERIAL AND METHODS

Different tree sensors were installed on three mature Rhizophora stylosa Griff. trees, similar in size, on North Stradbroke Island in Australia, a sand island in the Moreton Bay. The study area was located on the bay side of the island, at 27° 27' 3.25"S and 153° 25' 47.70"E (Figure 1). In the study area, the three trees were located in the central part of a mangrove forest strip. The elevation of the land was approximately 1.8 m above sea level. Meteorological data was collected from two meteorological stations. Solar radiation, air temperature (T), atmospheric relative humidity (RH) and rainfall were measured every 15 minutes, during day of year (DOY) 223 – 286 in 2013. Vapor pressure deficit (VPD) was derived from T and RH according to Buck (1981).

![Figure 1. Location of the field study on North Stradbroke Island and a schematic of the positioning of the different measured trees.](image)

Variations in stem radius were measured every 15 minutes using automated dendrometers (DRL 26 - Logging Band Dendrometer, ICT International). Sap flow was measured with HRM (Heat Ratio Method) sap flow sensors (ICT International) and branch water potential was measured with stem psychrometers (ICT International). Stomatal resistance was measured with a porometer (AP4 porometer, Delta-T Devices Ltd). The experiment ran from DOY 223-286.
Results

Measured diel sap flow was similar in all trees and the pattern consisted of a rise in sap flux density in the morning when transpiration started, typically a maximum around midday (4.7 ± 0.3 cm$^3$ cm$^{-2}$ h$^{-1}$) and a decrease in sap flux density in the afternoon. During the night sap flux density was usually slightly higher than zero (0.2979 ± 0.0009 cm$^3$ cm$^{-2}$ h$^{-1}$).

Branch water potential reached values as low as -4.28 MPa and as high as -0.56 MPa. The common pattern described in literature (Kume et al. 2007) and encountered in *R. stylosa* shows a decline when transpiration starts, which implies a force exerted on the water column due to transpiration. A minimum value is reached around midday after which the water potential starts to rise again. Throughout the night, the water potential keeps on rising, but at a slower rate until a new day starts and another cycle is initiated.

Both sap flux density and branch water potential exhibited the same classical patterns as other trees and had similar values as other mangrove species (Scholander 1968, Hao et al. 2009). The stomatal behavior of *R. stylosa* was also similar to other tree species using a C$_3$ metabolism for photosynthesis (Ibrahim et al. 2008). This behavior consists of stomatal closure during the night, opening during the day and possibly in case of stress partial midday stomatal closure in order to reduce transpiration (Ibrahim et al. 2008).

The long-term pattern in SDV consisted of periods of gradual growth, often followed by a steep decline. Periods of high stem swelling occurred when rainfall was registered. Only one out of three trees was able to enlarge its final stem diameter across the measurement period. This reflects the stressful conditions the trees endured, which is supported by the extreme dry conditions during the experiment with no single rain event in August whereas on average August has 5-10 days of rainfall in this area (61 mm) (data of Australian Bureau of Meteorology).

**Figure 2.** SDV pattern for each individual tree. Rain is shown with bars.
For each hour of the day an average growth value was calculated for the entire measurement period for all trees and these values were cumulated to generate an average daily growth pattern (Figure 3). This growth pattern highlights that *R. stylosa* showed a completely different typical day and night cycle compared to other tree species. This pattern was consistent throughout the entire measurement period and showed three distinct phases. The first phase started at sunrise whereby the stem radius expanded until midday. During the second phase in the afternoon the tree diameter shrunk until some time after dusk. During the third phase, after dusk, *R. stylosa* did not swell nor shrink. Growth per hour was highest during the first hours after sunrise, after which it slowed down and gradually changed in shrinkage, which occurred after midday. After dusk, the stem diameter remained nearly constant.

![Average growth per hour of all trees for the entire measuring period is shown with black circles ( ). A typical growth pattern is constructed by cumulating growth per hour, displayed by white circles ( )](image.png)

**Figure 3.** Average growth per hour of all trees for the entire measuring period is shown with black circles ( ). A typical growth pattern is constructed by cumulating growth per hour, displayed by white circles ( ). Shaded and unshaded areas represent nighttime and daytime, respectively.

For further elaboration of this peculiar SDV pattern, growth per day and growth before and after midday is displayed (Figure 4). In most cases, very negative radial stem growth followed days with positive growth.
Figure 4a). Three growth outliers were observed, on the days with rainfall, illustrating the importance of rainfall for the trees.
Figure 4b shows periodic growth (positive values) and shrinkage (negative values) according to the growth and shrinkage phase inferred from Figure 3.

Figure 4b shows that the average growth pattern constructed in Figure 3 is valid for nearly every single day because generally growth values were positive before midday and negative after midday. Furthermore, for each day growth between 6 h and 12 h was nearly equal to growth from 0 h till 12 h and shrinkage between 12 h and 20 h was nearly equal to growth from 12 h till 24 h. This confirms the growth pattern shown in Figure 3 consisting of radial stem growth from 6 h till 12 h, shrinkage from 12 h till 20 h and a constant diameter during the night. Therefore, the growth pattern of *R. stylosa* can be characterized by the growth dynamics taking place during the daytime, from 6 h till 20 h.
Figure 4. (a) Daily radial stem growth from 0 h to 24 h. (b) Radial stem growth between 0 h and 12 h is represented with black circles (●) and radial stem shrinkage between 12 h and 24 h is represented with white circles (○).

**DISCUSSION**

So far only few studies used automated band dendrometers to quantify mangrove growth (Krauss et al. 2007) and none of these studies measured short-term diel growth patterns. During this field trial, the trees clearly suffered from stress, especially during the first 20 days, indicated by the overall stem diameter shrinkage. Days with extensive shrinkage (Figure 4a) could be linked with an increase in average VPD compared to the previous day (>0.2 kPa), giving rise to higher transpiration rates. Days with extensive growth occurred only when rainfall provided fresh water, outlining the importance of rainfall as a fresh water source for growth of mangroves. While the diel patterns in sap flux density (Kume et al. 2007) and water potential (Kume et al. 2007) were comparable to the observations in several other species, an atypical sequence of shrinkage and growth was observed in
R. stylosa. Moreover, the cycle was opposite to the typical cycle defined by Downes et al. (1999). In fact, the growth pattern has more similarities with plants operating with CAM (Crassulacean Acid Metabolism) (Matimati et al. 2012). Yet, experiments by Andrews et al. (1984) and the stomatal conductance pattern measured in this study prove that R. stylosa is a C₃ plant.

The SDV pattern of R. stylosa is hence very exceptional, because SDV of all C₃ plants monitored so far have had the same dynamics in SDV. Therefore, we speculate that the mechanism giving rise to this extraordinary growth pattern is osmotically regulated. The strong growth following sunrise could be the consequence of osmotic substances formed during the first hours of the day lowering the water potential inside the cells and resulting in an influx of water to these cells. Due to dilution of these substances and a decrease in water potential of the atmosphere, swelling stops and the transpirational demand becomes so high that shrinkage starts. Because the strong growth and the start of photosynthesis coincide we suggest that the osmotic substances are formed through photosynthesis, e.g. osmotically active sugars (De Schepper et al. 2013).

Advantages of such a system would be that cells operate at a higher water content during the day which improves the performance of processes such as cell expansion, cell wall formation and photosynthesis (Porporato et al. 2001). This provides many benefits compared to other species, which could partially explain the success of R. stylosa in thriving in saline environments.

CONCLUSION

Unexpectedly, a radial stem growth pattern was measured that is markedly different from other (mangrove) species. Although more research is required to elucidate the physiological behaviour of R. stylosa, it seems most likely that this pattern originates from a clever osmotic regulation mechanism. This enables R. stylosa to thrive in a challenging environment defined by salt and physiological drought stress. Further research should clarify whether the pattern always exists in R. stylosa and if osmotic regulation truly occurs.

ACKNOWLEDGEMENTS

We thank Matthew Hayes, Nina Welti, Stefanie De Groote, Mieke Van Houtte and Niels De Baerdemaeker for their indispensable assistance during the fieldwork. The Commission for Scientific Research (CWO) of Ghent University has provided travel grants to SdG, MvH, NdB and the first author. We are indebted to the Moreton Bay Research Station, University of Queensland for their technical support. The National Centre for Groundwater Research and Training is a co-funded Centre of Excellence of the Australian Research Council and the National Water Commission.

REFERENCES


