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Hydraulic architecture of the mangrove *Rhizophora mucronata* under different salinity and flooding conditions.

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Introduction

Mangroves are (sub)tropical forests occurring in the intertidal areas of coastal shorelines protected from wave action. This saline habitat implies that these trees experience a perpetual physiological drought. Consequently, mangrove trees are at risk of drought-induced cavitation. A question which immediately presents itself is “How do mangroves safeguard the water transport under these stressful conditions”. This question can be dealt with by studying xylem anatomy. In particular, vessel density and diameter are frequently mentioned in relation to cavitation susceptibility. High vessel density creates a redundancy in the transport system which increases the conductive safety. According to the air-seeding hypothesis, the advantage of small vessels is a high cavitation resistance due to the association with small pit pore diameters within a species (Tyree and Sperry 1989, Lo Gullo and Salleo 1990, 1993).

This study focuses on the mangrove species *Rhizophora mucronata* (Rhizophoraceae) from Kenya, in which annual growth rings were recently detected (Verheyden et al. 2004). The rings are formed by a gradual change in vessel density. A zone of low vessel density is produced during the rainy season (earlywood), while a zone of high vessel density was found to be associated with the dry season (latewood) (Verheyden et al. 2004). It is important to note that the identification of annual growth rings now enables us to account for the inter- and intra-annual variability when studying vessel characters in mangroves (see Verheyden et al. 2005). Although salinity is a determining factor for the regulation of the water transport in mangroves (Naidoo 1985, 1986, Clough and Sim 1989, Zimmermann et al. 1994, Ball et al. 1997), the influence of salinity on vessel density and diameter remains to be demonstrated.

Aims and methods

The aim of this study was to investigate the relationship between vessel features, in particular vessel density and diameter, and site-specific environmental conditions. Fifty wood discs from eight sites in Gazi Bay (39°30’E, 4°25’S), Kenya, differing in salinity (Salinity category 1-6, covering a salinity range from 26.4 to 49.2) and inundation class (class 1-4) were considered. In addition to vessel density, both tangential and radial diameter were measured directly on the sanded stem discs making use of digital image analysis software

(AnalySIS Pro v.3, Soft Imaging System GmbH, Münster, Germany). Moreover, inter-annual variability was excluded by focusing on one distinct year and intra-annual variability is considered by separating the early- and latewood (Fig. 1) (except for SAL5, in which growth rings were too narrow to differentiate early- from latewood).

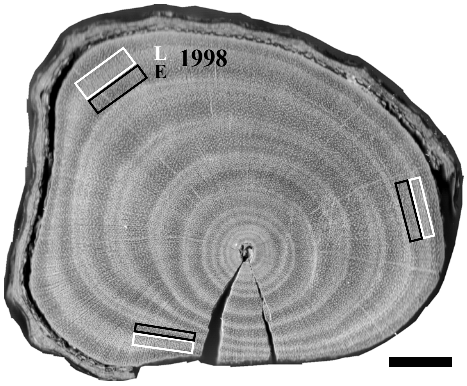

Figure 1: Wood anatomical measurements were carried out at three positions, chosen along a radius of high, moderate and slow growth rate. At each position two quadrats (size is exaggerated for clarity) covering earlywood (E) and latewood (L) of the year 1998 were studied. Scale bar: 1cm. Specimen number Tw56722, part of the Tervuren wood collection.

The effect of growth rate on the vessel features was examined by comparing vessel characters with ring width along three different radii per specimen. Finally, results were statistically analysed making use of a "repeated measures analysis of variance" and a t-test for dependent samples, carried out in STATISTICA 7.0 (StatSoft Inc., Tulsa, USA).

Results and discussion

The effect of salinity

A major correlation was observed between vessel density and salinity (Fig. 2), both in rainy (ANOVA: $F=3.45$, $p<0.05$) and dry season ($F=3.24$, $p<0.05$). In Fig. 2, (as well as in Fig. 3, see further) the use of the average of the three positions was appropriate since the analysis of variance did not show a growth rate effect for either salinity or inundation class, irrespective of vascular traits (rainy season: F=2.57/0.69, 0.11/0.095, 1.52/1.87; p=ns; dry season: F=1.35/0.52, 0.018/0.088, 0.36/0.078; p=ns, for respectively vessel density, tangential and radial vessel diameter). In addition, vessel density and seasons were shown to be tightly coupled ($t=13.31$, $p<0.0001$). A strong evaporation results in an increasing salinity, which leads to a higher vessel density at each site (Fig. 2).

In this way, the findings of the previous study on *R. mucronata* carried out at one site (Verheyden et al. 2005) are validated. It is hypothesized that the adjustment in vessel density allows *R. mucronata* to withstand the negative effects of a spatial as well as a temporal varying salinity, regarding an adequate water balance. Although water is not a limiting factor in the mangroves, the salt concentration causes a serious stress by creating a physiological drought (Clough and Sim 1989).

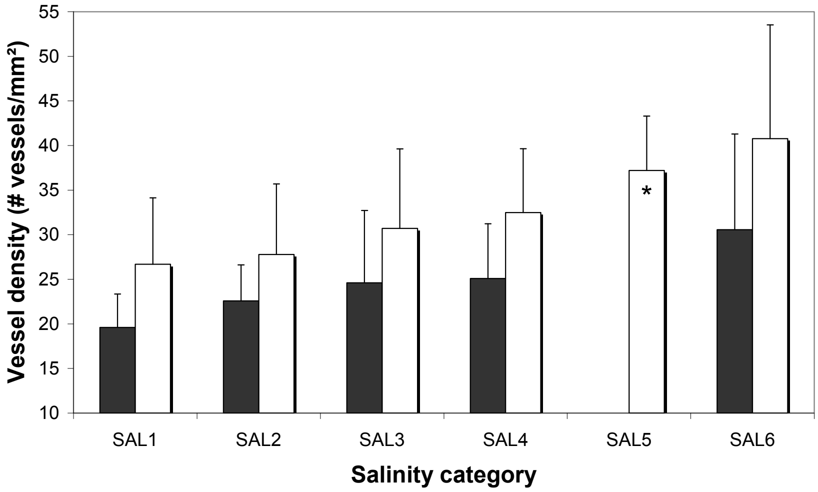

*Figure 2: Mean vessel density in relation to salinity for both rainy season (dark bars) and dry season (light bars). * This category represents the annual average vessel density since growth rings were too narrow to differentiate between dry and rainy season (see also Aims and Methods). Error bars correspond to standard deviations.*

Consequently, the water transport in mangroves is at risk of drought-induced cavitation. A high vessel density offers a double advantage with respect to conductive safety. First, when the same number of vessels is cavitated, a higher percentage of the transport system remains functional in high vessel density compared to low vessel density wood (Baas *et al.* 1983, Villar-Salvador et al. 1997). Second, a high proportion of vessels are in contact with each other via intervessel pits since vessels do not follow a straight line but twist along their path (Kitin et al. 2004). Therefore, embolized vessels can be circumvented by means of the high number of alternative routes for the water transport.

In contrast to vessel density, tangential vessel diameter was found to be extremely constant. Neither salinity ($F=0.41$ and 1.28, $p=ns$, for rainy and dry season respectively), nor seasonal fluctuations ($t=1.85$, $p=ns$) turned out to have any impact. Moreover, the striking similarity between the frequency distributions for different salinity categories, stress the invariable nature of the tangential vessel diameter (Fig. 3a).

Interestingly, although not statistically significant ($F=1.11$ and 2.04, $p=ns$ for rainy and dry season respectively), radial diameter does show a tendency to be smaller at sites with a high salinity (Fig. 4). This declining trend is supported by a slight shift in size distribution towards narrower vessels when salinity is increased (Fig. 3b). A difference between dry and rainy season was recorded but is not well expressed ($t=-2.5$, $p<0.02$).

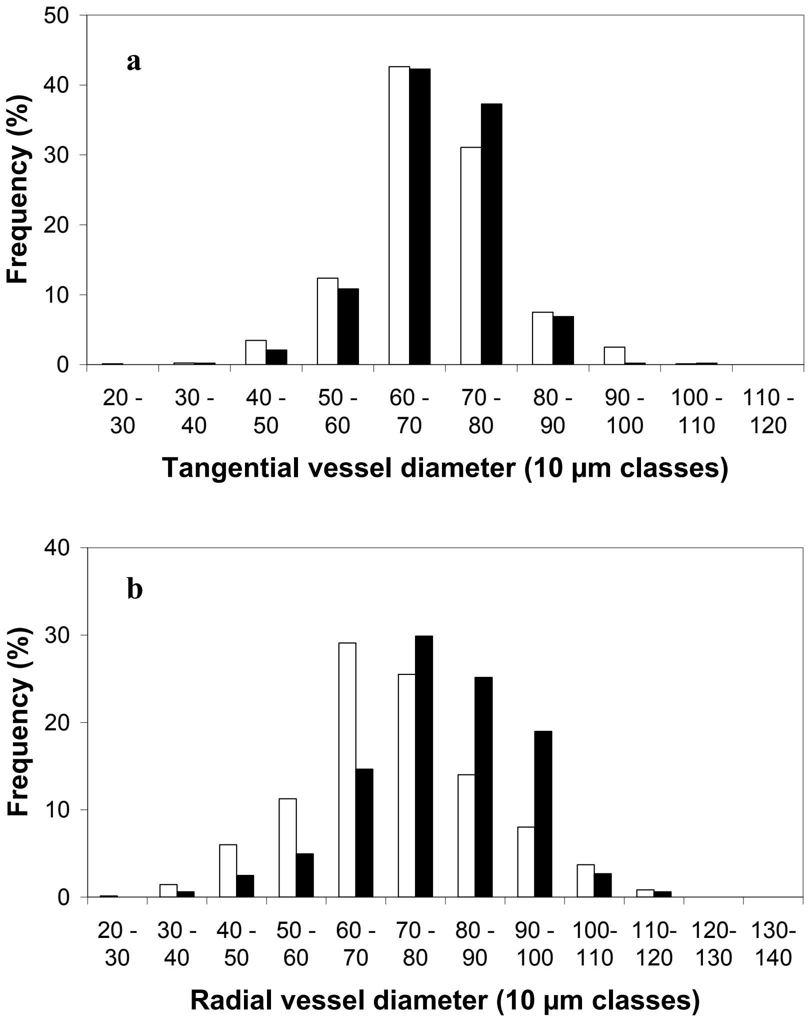

Figure 3: Frequency distribution of (a) tangential and (b) radial diameter of wood samples originating from sites with contrasting salinity (SAL2-SAL5) and inundation classes (class 1-class 4). Dark bars: SAL2, inundation class 1. Light bars: SAL5, inundation class 4.

Several studies report a link between drought and narrow conduits (*e.g.* Lo Gullo et al. 1995, Villagra and Roig Juñent 1997, Arnold and Mauseth 1999, Corcuera et al. 2004, Stevenson and Mauseth 2004), which was not found here. The presence of two diameter classes in the xylem vessels is a frequent observation of the arid flora (Baas et al. 1983, Baas and Schweingruber 1987, Villagra and Roig Juñent 1997) for it combines an efficient (large vessels) with a safe (small vessels) water transport system (Mauseth and Stevenson 2004). However, as the unimodal diameter distribution (Fig. 3) demonstrates, the absent trend with salinity and inundation class can not be attributed to the interference of a vessel dimorphism. Longer and wider vessels are usually produced in the lower parts of a tree with age, to maintain a favourable water balance when growing and increasing its leaf surface (Tyree and Ewers 1991, Hudson et al. 1998, Cruiziat et al. 2002). Mangrove trees, with the smallest average diameter (SAL5, Fig. 3-4), are noted to have the highest cambial age. Vessel diameter is therefore shown to be influenced by salinity more then by age.

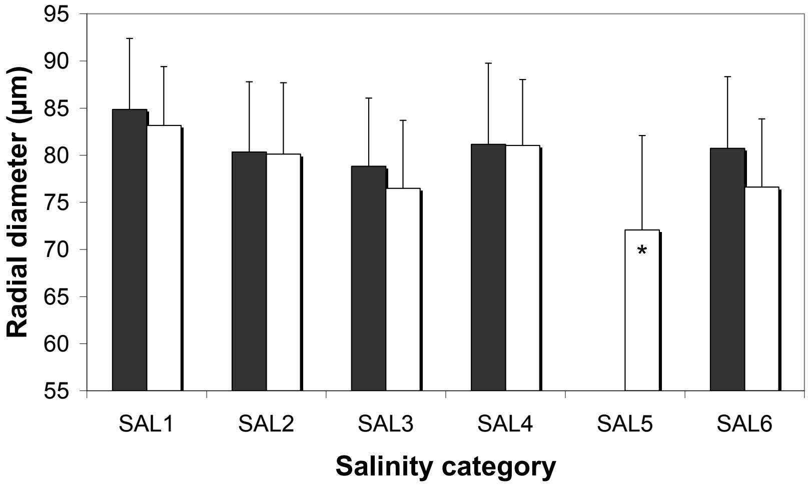

*Figure 4: Mean radial vessel diameter in relation to salinity for both rainy season (dark bars) and dry season (light bars). * This category represents the annual average radial vessel diameter since growth rings were too narrow to differentiate between dry and rainy season (see also Aims and Methods). Error bars correspond to standard deviations.*

The increased vessel density with salinity and inundation class, not coinciding with a pronounced decrease in vessel diameter, indicates a lack of a trade-off between conductive safety and efficiency. According to the air-seeding hypothesis, small vessel diameters can be associated with small pit pore diameters within a species, and thus to cavitation resistance (Tyree and Dixon 1986, Tyree and Sperry 1989, Lo Gullo and Salleo 1991, 1993). Therefore, declining vessel dimensions with an increase in water stress were expected. However, only a marked increase in vessel density was recorded, which possibly balances out the greater susceptibility to cavitation due to the almost steady diameters. However, the relationship between vessel and pit pore diameter is still subject of investigation, and cavitation susceptibility is generally dependent of the pore diameter of the pits (Sperry and Tyree 1988, Tyree and Sperry 1989, Jarbeau et al. 1995, Cruiziat et al. 2002). In this context, a varying pit pore diameter, independent of vessel diameter, is proposed as an alternative explanation for the quasi-invariable vessel size.

The effect of inundation class

With respect to inundation class a positive relationship was found with vessel density ($F=7.91$, $p<0.002$ and $F=7.51$, $p<0.01$ for rainy and dry season respectively); similar to our findings for the salinity-effect. The highest vessel density occurred at inundation class four (Fig. 5), which can be explained by the associated poikilohaline conditions. The exposure to cavitation associated with a fluctuating salt concentration exceeds the one resulting from a constant salinity, of the average and in some cases even the maximum salinity value of the fluctuation (Lin and Sternberg 1993, Yáñez-Espinosa and Terrazas 2001).

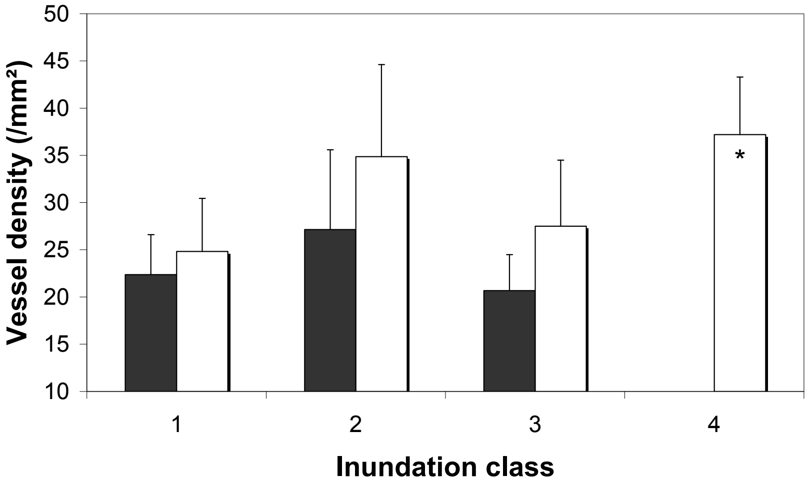

*Figure 5: Mean vessel density in relation to inundation class for both rainy season (dark bars) and dry season (light bars). * This category represents the annual average vessel density since growth rings were too narrow to differentiate between dry and rainy season (see also Aims and Methods). Error bars correspond to standard deviations.*

The positive trend in vessel density with inundation class is interrupted at inundation class three (Fig. 5). It is assumed that the low vessel density is a reflection of the low salinity (SAL1 and SAL2) at these sites. Concerning vessel diameter, only annual averages of radial diameter are significantly smaller at higher inundation class ($F=3.36$, $p<0.02$). However, a pronounced shift in size distribution is observed when SAL2 and SAL5 are compared (Fig. 3b), which can most likely be ascribed to the interplay with contrasting inundation classes (class 1 and 4).

Conclusion and perspectives

There has been much interest in the ecology of mangroves in general, but their hydraulic architecture received less attention. The plasticity in vessel characters of *R. mucronata* in response to the prevailing climate conditions was reported earlier by means of a time series analysis (Verheyden et al. 2005). In the present study, these findings have been validated on a larger sample size, representing different environmental conditions. In particular, the seasonal difference in vessel density was confirmed and the relation between salinity and vessel density was demonstrated. In addition, the absent growth rate effect strengthens its potential as an environmental proxy. Finally, our results are especially motivating for future studies concerning intervessel pits. We suggest variability in pore diameter can offer an explanation for the almost invariable nature of vessel dimensions. Investigation of the pits is unfortunately a delicate one. Several artefacts have to be taken into consideration (Choat et al. 2003, 2004), which may however not be a drawback but may encourage further efforts.

Acknowledgements

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