# Influence of a Salinity Gradient on the Vessel Characters of the Mangrove Species *Rhizophora mucronata*

NELE SCHMITZ[1,2,*], ANOUK VERHEYDEN[2,†], HANS BEECKMAN[2],
JAMES GITUNDU KAIRO[3] and NICO KOEDAM[1]

[1]*Vrije Universiteit Brussel (VUB), Laboratory for General Botany and Nature Management (APNA), Pleinlaan 2, 1050 Brussels, Belgium,* [2]*Royal Museum for Central Africa (RMCA), Laboratory of Wood Biology and Wood Collection, Leuvensesteenweg 13, 3080 Tervuren, Belgium and* [3]*Kenya Marine and Fisheries Research Institute (KMFRI), PO Box 81651, Mombasa, Kenya*

● *Background and Aims* Although mangroves have been extensively studied, little is known about their ecological wood anatomy. This investigation examined the potential use of vessel density as a proxy for soil water salinity in the mangrove species *Rhizophora mucronata* (Rhizophoraceae) from Kenya.
● *Methods* In a time-standardized approach, 50 wood discs from trees growing in six salinity categories were investigated. Vessel densities, and tangential and radial diameters of rainy and dry season wood of one distinct year, at three positions on the stem discs, were measured. A repeated-measures ANOVA with the prevailing salinity was performed.
● *Key Results* Vessel density showed a significant increase with salinity, supporting its use as a prospective measure of salinity. Interestingly, the negative salinity response of the radial diameter of vessels was less striking, and tangential diameter was constant under the varying environmental conditions. An effect of age or growth rate or the presence of vessel dimorphism could be excluded as the cause of the absence of any ecological trend.
● *Conclusions* The clear trend in vessel density with salinity, together with the absence of a growth rate and age effect, validates the potential of vessel density as an environmental proxy. However, it can only be used as a relative measure of salinity given that other environmental variables such as inundation frequency have an additional influence on vessel density. With view to a reliable, absolute proxy, future research should focus on finding wood anatomical features correlated exclusively with soil water salinity or inundation frequency. The plasticity in vessel density with differing salinity suggests a role in the establishment of a safe water transport system. To confirm this hypothesis, the role of inter-vessel pits, their relationship to the rather constant vessel diameter and the underlying physiology and cell biology needs to be examined.

**Key words:** *Rhizophora mucronata*, mangrove, ecological wood anatomy, vessel density, vessel diameter, proxy, salinity, inundation frequency, Kenya, hydraulic architecture.

## INTRODUCTION

Mangroves are tropical and subtropical forests occurring in the intertidal areas of coastal shorelines protected from wave action. Mangrove forests provide a plethora of ecosystem services and products and play an important socio-economic as well as ecological role (Rönnbäck, 1999; Dahdouh-Guebas *et al.*, 2000, 2005; Kairo *et al.*, 2001; Moberg and Rönnbäck, 2003). World-wide disappearance of mangrove forests is undoubtedly mainly caused by large-scale clear cutting and land conversion (Valiela *et al.*, 2001; FAO, 2003). However, changing environmental conditions, in particular salinity, can also lead to mangrove degradation and die-off (Spalding *et al.*, 1997; Kathiresan, 2002). Changes in soil water salinity can be influenced by climate (Drexler and Ewel, 2001) as well as by human impacts caused by leakage from salt extraction pans or by the damming or redirection of rivers (Kovacs *et al.*, 2001; Alongi, 2002). Nevertheless, relating mangrove degradation to changes in soil water salinity is still impeded by a lack of local, long-term environmental

data (Kovacs *et al.*, 2001). Performing salinity measurements on a long-term basis is impractical as the spatial and temporal variations in the mangrove habitat (cf. Ridd and Renagi, 1996; Ball, 1998; Matthijs *et al.*, 1999; Marchand *et al.*, 2004) would require a high sampling intensity. Therefore, there is an urgent need for proxies of environmental conditions and in particular of salinity.

Recently, the presence of annual growth rings was discovered in the mangrove *Rhizophora mucronata* from Kenya (Verheyden *et al.*, 2004) and *R. mangle* from northern Brazil (Menezes *et al.*, 2003). The annual rings are composed of a zone of low vessel density and a zone of high vessel density, which are produced during, respectively, the rainy season (earlywood) and dry season (latewood) (Verheyden *et al.*, 2004). Verheyden *et al.* (2005) further suggested that wood anatomical features in *R. mucronata* could be a potential proxy for past environmental conditions. In particular, temporal changes in soil water salinity might be recorded in vessel density (Verheyden *et al.*, 2005) through the effect of salinity as a determining factor for the regulation of water transport in mangroves (Naidoo, 1985, 1986; Clough and Sim, 1989; Lin and Sternberg, 1993; Zimmermann *et al.*, 1994; Sobrado, 2001; Paliyavuth *et al.*, 2004; Lopez-Portillo

* For correspondence. E-mail nschmitz@vub.ac.be
† Present address: Department of Biology, SUNY Orange County Community College, 115 South Street, Middletown, NY 10940, USA.

TABLE 1. *Characteristics of the studied* Rhizophora mucronata *specimens and the different sampling sites*

| Site* | $n$ | Tw number[†] | Age (years)[‡] | Salinity (‰)[§] | Salinity category[¶] | Inundation class** |
|---|---|---|---|---|---|---|
| 1 | 10 | 55904 to –08, 56705 to –09 | 9–16 | 26·4 | 1 | 3 |
| 2 | 5 | 56710 to –14 | 17–37 | 31·9 | 2 | 3 |
| 3 | 4 | 55883 to –86 | 11–22 | 33·6 | 2 | 1 |
| 4 | 5 | 55872, –73, –76, –80, –81 | 17–33 | 35·2 | 3 | 2 |
| 5 | 5 | 55958, –75, –78, –90, –91 | 4–5 | 35·4 | 3 | 3 |
| 6 | 10 | 55890 to –94, 56725 to –29 | 11–24 | 38·2 | 4 | 2 |
| 7 | 7 | 55887 to –89, 56730, –33, –34, –36 | 25–57 | 42·7 | 5 | 4 |
| 8 | 4 | 56721 to –24 | 4–20 | 49·2 | 6 | 2 |

* See also Fig. 1.
[†] Accession number of the samples in the Tervuren wood collection.
[‡] Cambial age in 1998.
[§] Soil water salinity at 10 cm depth, data from Verheyden (2004).
[¶] Salinity categories (see Materials and methods).
** Inundation class according to Watson (1928) in Macnae (1968).

*et al.*, 2005). However, precipitation, which was taken as a measure of salinity, exhibited the lowest correlation coefficient with vessel density (Verheyden *et al.*, 2005). The authors suggested that the low correlation might be due to environmental and climatic factors interfering with the salinity–rainfall relationship. During the rainy season, salt is flushed not only directly by rainfall but also by land run-off, groundwater flow and river input, all related to the topography of the environment (Ewel *et al.*, 1998; Hoguane *et al.*, 1999). Other determinants of salinity are the water retention capacity of the soil (Wiemann *et al.*, 1998), evaporation intensity (Naidoo, 1989) and tidal inundation (Lin and Sternberg, 1992, 1993; Passioura *et al.*, 1992). The effect of salinity *per se* on vascular features still needs to be demonstrated (Verheyden *et al.*, 2005).

The present study investigated the potential of vessel features as a proxy for soil water salinity in the mangrove species *R. mucronata* in Gazi Bay, Kenya. Time series of data records of salinity *per se* are not available for the study area, hampering investigations of the effect of temporal changes in salinity on vessel features. As an alternative, a time-standardized measuring approach is used to allow an accurate comparison between spatial differences in soil water salinity and vessel density and diameter. In this way, information will be indirectly gained regarding their proxy potential to trace temporal changes in salinity.

## MATERIALS AND METHODS

### Study sites and sample collection

The study sites are located in the mangrove forest of Gazi Bay (39°30′E, 4°25′S), situated approx. 50 km south of Mombasa, Kenya. Two seasonal rivers discharge into the bay and provide a freshwater source for the mangroves: the Mkurumuji and the Kidogoweni (Kitheka, 1997).

Wood discs from the trunk of 50 trees (now part of the wood collection of the Royal Museum for Central Africa, Tervuren, Belgium; for accession numbers see Table 1) of *Rhizophora mucronata* Lam. were collected in October 1999 and May 2002. Tree diameters at 1·3 m height varied between 2 and 10 cm and were associated with a cambial
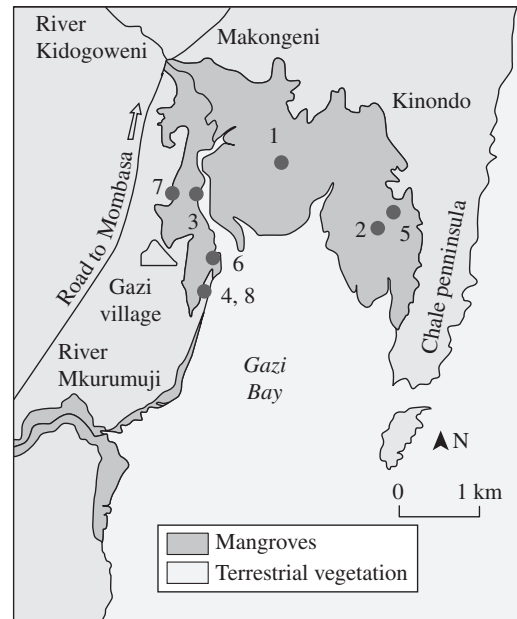


FIG. 1. Map of the study site, Gazi Bay (Kenya), indicating the different sites where wood discs were collected. Sites four and eight are only 20 m from each other but site four is at the fringe and site eight in the middle of a basin forest (see also Table 1) (adapted from UNEP, 2001).

age in 1998 of 4–57 years (Table 1). The trees originate from eight sites (4–10 trees per site), selected for their differences in salinity and inundation class (Fig. 1, Table 1). Soil water was collected in 1998, 1999 and 2002 at 10 cm depth using a punctured plastic tube connected to a vacuum pump. At each site, 1–3 salinity measurements were carried out with a WTW P4 multiline conductivity meter (Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany). Within the studied mangrove stands, soil water salinity ranged from 26·4 to 49·2 ‰, which is the upper limit of distribution of *R. mucronata* in Gazi (data from Verheyden, 2004). Sites were divided into six salinity categories (SAL1–SAL6); sites two and three as well as sites four and five were combined (Table 1). This was justified as there was no statistical difference between
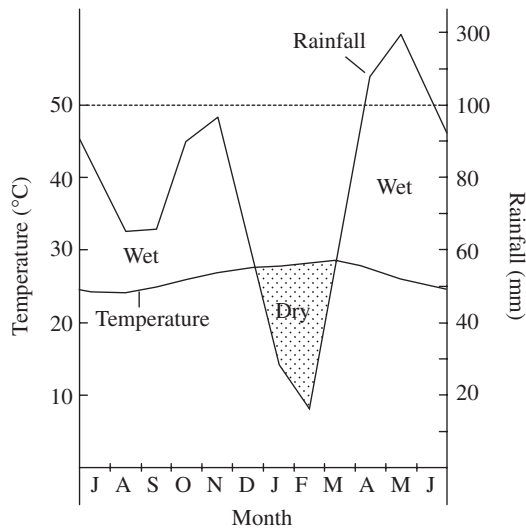
FIG. 2. Climate diagram of Mombasa (39°36′E, 4°0′S) adapted from Lieth *et al.* (1999), showing the long (April–July) and short (October–November) rainy season and one distinct dry season (January–February). Dotted area, dry season; plain white area, wet season. The precipitation axis is reduced to one-tenth scale above the dotted horizontal line.
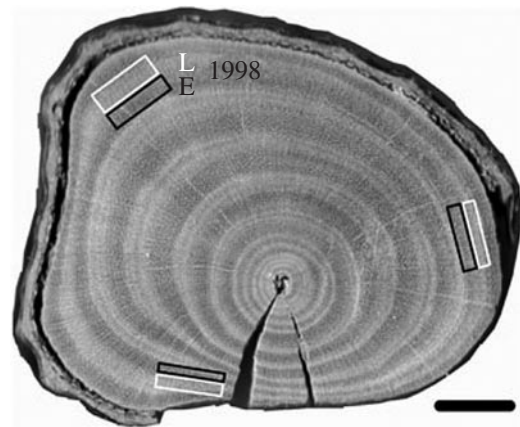


FIG. 3. Wood anatomical measurements were carried out in a time-standardized way. At three positions, chosen along a radius of high, moderate and slow growth rate, two quadrats (size exaggerated here for clarity) covering rainy season wood (earlywood, E) and dry season wood (latewood, L) of the year 1998 were studied. Scale bar = 1 cm. Specimen number Tw56722, part of the Tervuren wood collection.

the combined sites [ANOVA, Tukey's honest significant difference (HSD) test]. Depending on the topography and the tidal range, zones of different inundation classes can be defined. Inundation classes one, two, three and four correspond to an area being inundated by, respectively, 100–76, 75–51, 50–26 and 25–5 % of the high tides (cf. Tomlinson, 1994).

### Climate description

The climate along the Kenyan coast is characterized by a bimodal distribution of precipitation, which results in a long rainy season (April–July), a short rainy season (October–November) and one distinct dry season (January–February) (Fig. 2). In accordance with earlywood formation (see Verheyden *et al.*, 2004), the term 'rainy season' will further be used to indicate the period of both the long and the short rainy season (April–November).

### Sample preparation and wood anatomical measurements

Wood samples were air-dried and sanded using a series of sandpaper from 100 to 1200 grit. Vessel features 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), at an optical magnification of ×12·5. Vessel density (number of vessels per mm$^2$) as well as average radial and tangential vessel diameter (µm) were measured at three positions on the wood disc. The size of the quadrats was chosen to include at least 20 vessels. Taking into account earlier findings on the temporal changes in vessel density in *R. mucronata* (Verheyden *et al.*, 2005), inter-annual variability was excluded by carrying out all measurements within the ring of the year 1998. The 1998 ring was the most recent ring that was fully developed in all samples (samples were

collected in 1999 and 2002). In addition, intra-annual variation was investigated by measuring the wood produced during the rainy season (earlywood, see Verheyden *et al.*, 2004) and the wood produced during the dry season (latewood) of the year 1998 separately (Fig. 3). However, for samples collected at site seven (corresponding to SAL5) earlywood and latewood could not be examined separately as growth rings were too narrow to allow differentiation. In order to include SAL5 in the statistical analysis and to allow study of the variability of vessel features along the maximum salinity and inundation frequency gradient, annual averages were calculated for each site and included in the statistical analysis. With regard to asymmetrical wood discs, the three measuring positions were chosen along the longest, smallest and medium axis of the wood disc (see Fig. 3). Consequently, by comparing the three positions from each specimen with ring width, the within-tree growth rate effect on vessel features could be investigated. The between-tree correlation between growth rate and vessel diameter was investigated as well. For this purpose, growth rate data were used from a cambial marking experiment on 20 of the studied trees (Verheyden, 2004).

### Statistical analysis

To trace trends in the three vessel characters considered, as a function of salinity and inundation class, a repeated-measures ANOVA was carried out in STATISTICA 7·0 (StatSoft Inc., Tulsa, OK, USA). Two separate analyses were performed, one with salinity and one with inundation class as a grouping factor. A combined analysis could not be performed as all salinity categories do not occur at each inundation class. Both an analysis based on annual averages and an analysis considering rainy and dry season wood separately ('season' as an additional categorical variable) were performed. Vessel density was inserted as a repeated-measures factor with three levels, as

T ABLE 2. *Repeated-measures ANOVA's of vessel density, radial and tangential diameter*

| Effect | Rainy season | | | Dry season | | | Annual average | | |
|---|---|---|---|---|---|---|---|---|---|
| | d.f.[‡] | MS[§] | F | d.f. | MS | F | d.f. | MS | F |
| Vessel density | | | | | | | | | |
| Salinity | 4 (38) | 2·78 (sqrt) | 3·44* | 4 (38) | 0·47 (ln) | 3·24* | 5 (44) | 0·14 (log) | 6·63*** |
| Position[†] | 2 | 0·41 (sqrt) | 2·57 | 2 | 0·04 (ln) | 1·35 | 2 | 0·01 (log) | 2·13 |
| Inundation class | 2 (40) | 0·89 (ln) | 7·92** | 2 (40) | 1·02 (ln) | 7·51** | 3 (46) | 1·54E-03 (in) | 10·07**** |
| Position | 2 | 0·02 (ln) | 0·69 | 2 | 0·02 (ln) | 0·52 | 2 | 3·09E-05 (in) | 0·86 |
| Tangential diameter | | | | | | | | | |
| Salinity | 4 (38) | 28·22 | 0·41 | 4 (38) | 60·26 | 1·28 | 5 (44) | 80·30 | 1·46 |
| Position | 2 | 1·84 | 0·12 | 2 | 33·72 | 2·06 | 2 | 22·46 | 1·46 |
| Inundation class | 2 (40) | 58·04 | 0·89 | 2 (40) | 17·37 | 0·35 | 3 (46) | 68·36 | 1·20 |
| Position | 2 | 1·57 | 0·10 | 2 | 23·48 | 1·37 | 2 | 12·32 | 0·76 |
| Radial diameter | | | | | | | | | |
| Salinity | 4 (38) | 147·47 | 1·11 | 4 (38) | 209·36 | 2·04 | 5 (44) | 392·78 | 3·36* |
| Position | 2 | 35·96 | 1·52 | 2 | 9·57 | 0·36 | 2 | 25·31 | 1·16 |
| Inundation class | 2 (40) | 272·72 | 2·14 | 2 (40) | 158·30 | 1·43 | 3 (46) | 561·12 | 4·75** |
| Position | 2 | 46·84 | 1·87 | 2 | 2·07 | 0·08 | 2 | 33·90 | 1·49 |

[†] Measurements were repeated at three positions on each stem disc (see Fig. 3).

[‡] Error given in parentheses

[§] Mean square (MS) with transformation type in parentheses: in = inverse, ln = natural logarithm, log = logarithm (common base 10), sqrt = square root.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

measurements were carried out at three positions within each wood sample (Portney and Watkins, 2000). *Post-hoc* comparisons between group averages were made with Tukey's HSD test for unequal group sizes, as recommended by Quinn and Keough (2002). A Student's *t*-test for dependent samples was used to search for differences in vessel diameter and vessel density between dry and rainy season within sites. When the Levene's test indicated heterogeneity of variances or the Shapiro–Wilk's *W* test showed a non-normal distribution, a common logarithmic, natural logarithmic, square root or inverse transformation was executed to comply with the assumptions of an ANOVA/*t*-test. Finally, a Pearson correlation coefficient was calculated between the log-transformed growth rate and the radial vessel diameter.

## RESULTS

The repeated-measures ANOVA did not show a within-tree positional effect for vessel density, tangential or radial vessel diameter, for either salinity or inundation class (Table 2). Therefore, the vessel density obtained from the three positions on the stem disc was averaged and this average was used for all subsequent figures.

A significant positive relationship between vessel density and salinity was found for the rainy (earlywood) as well as for the dry season (latewood) (Fig. 4A, Table 2). This positive relationship was maintained when vessel densities were averaged (annual averages in order to include SAL5, see Materials and methods) (Table 2). A distinctly lower vessel density was recorded at the sites with low salinity, relative to the sites with high salinity (SAL1 to SAL3 vs. SAL5, $P < 0.001$, 0·01, 0·05, respectively), as shown by Tukey's HSD test.

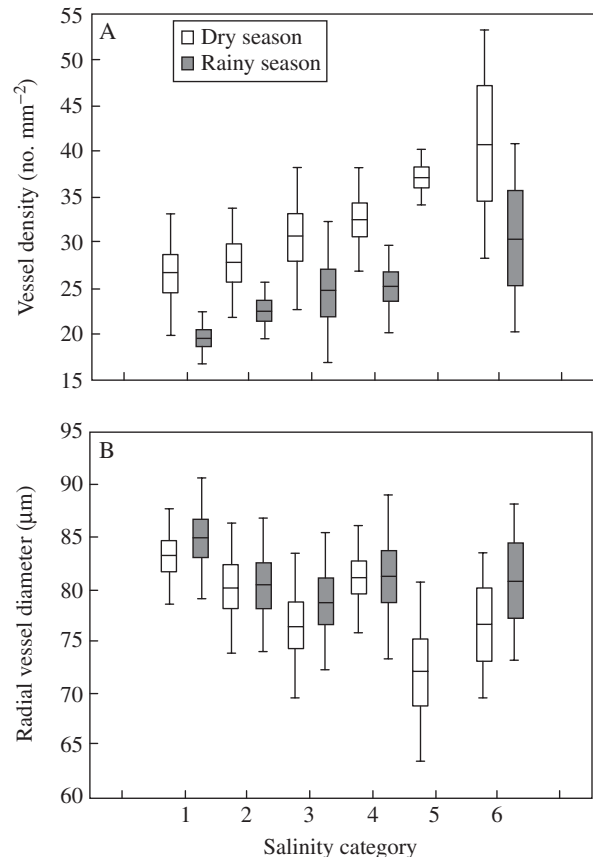In contrast to vessel density, no significant effect of salinity on the radial and tangential diameter was found in



F IG . 4. (A) Mean vessel density and (B) mean radial vessel diameter in relation to salinity for both rainy and dry seasons. Salinity category five represents the annual average value of the respective vessel feature as growth rings were too narrow to differentiate rainy season and dry season wood (see also Materials and Methods). Line, mean; box, standard error; whiskers, s.d.
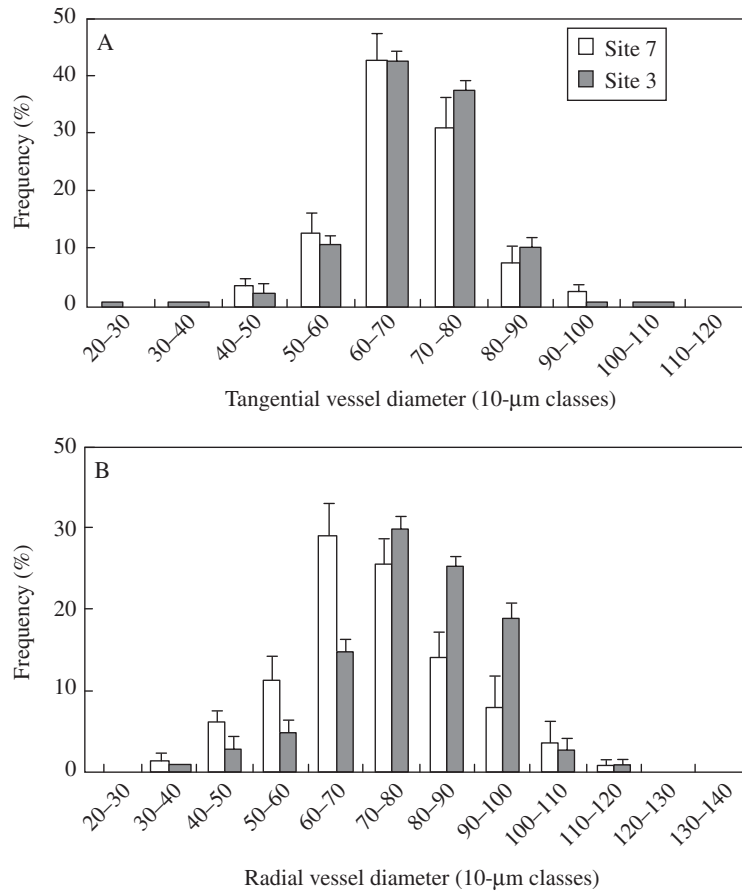
FIG. 5. Frequency distributions of the vessels, according to their (A) tangential and (B) radial vessel diameter (10-μm classes) for sites seven and three (see also Table 1, Fig 1), representing contrasting salinity categories (SAL2 and SAL5) and inundation classes (one and four). Error bars correspond to s.e.

TABLE 3. *Vessel characteristics for earlywood and latewood (values are means of all six salinity categories) and results for the* t-*test for dependent samples (*n = *129)*

| Variable | Rainy season Mean ± s.d. (range) | Dry season Mean ± s.d. (range) | t-test |
|---|---|---|---|
| Vessel density (no. of vessels mm$^{-2}$) | 23 ± 7 (11–57) | 30 ± 9 (14–66) | $t = 13\cdot31\ P < 0\cdot0001$ |
| Radial diameter (μm) | 81·26 ± 7·81 (30·30–134·99) | 79·87 ± 7·38 (30·30–132·23) | $t = -2\cdot50\ P = 0\cdot01$ |
| Tangential diameter (μm) | 71·32 ± 5·73 (33·06–115·7) | 70·72 ± 5·36 (35·81–115·7) | $t = 1\cdot85\ P = 0\cdot07$ |

either rainy or dry season wood (Table 2). The invariable nature of the tangential diameter was further expressed in the size distribution (Fig. 5A). By contrast, a slight decline in radial diameter was observed at increased salinity (Fig. 4B), which was supported by a significant relationship for the annual averages (Table 2) and a shift in the size distribution from SAL2 to SAL5 (Fig. 5B). Differences in vessel features between rainy season and dry season were significant for vessel density and radial diameter, but not for tangential diameter (paired *t*-test, Table 3).

Similar to the results obtained for salinity, a positive significant relationship was found between vessel density and inundation class (and for annual averages) as well as for rainy and dry season measurements (Table 2). This relationship was most prominent when comparing class one vs. class four ($P < 0\cdot05$, Tukey's HSD test). However, there was a considerably lower vessel density at inundation class three compared with at inundation classes two and four (d.f. = 46, $P < 0\cdot01$ and $0\cdot002$, respectively, Tukey's HSD test), which interrupts the positive trend. With regard to vessel diameter, a significant relationship with inundation class was only detected for the annually averaged radial diameter (Table 2) although a trend in the data could not be detected visually.

## DISCUSSION

Vessel density increases from low- to high-salinity areas in the *R. mucronata* mangrove forest of Gazi (Fig. 4A), in accordance with observations for the mangrove-associated

*Annona glabra* (Yáñez-Espinosa and Terrazas, 2001). Similar to earlier findings (Verheyden *et al.*, 2004, 2005), a higher vessel density was also found in the dry season as compared with the rainy season (Fig. 4A, Table 3), suggesting that vessel density can be used as an indicator for temporal changes in salinity. Indeed, seasonal fluctuations in vessel density can be partly attributed to an increase in salinity from the rainy to dry season. Other seasonal factors possibly affecting vessel density are phenology (Slim *et al.*, 1996; Drew, 1998; Salleo *et al.*, 2003; Choat *et al.*, 2005; Coupland *et al.*, 2005), together with nutrients (February and Manders, 1999; Alongi *et al.*, 2005), and water availability. A relatively higher vessel density is observed in the xylem of xerophytes compared with the vegetation of more mesic environments (Baas *et al.*, 1983; Carlquist and Hoekman, 1985; Lindorf, 1994). Interestingly, Yáñez-Espinosa *et al.* (2001) found no differences in vessel number between different sites with presumed different soil water salinity (based on soil texture) in their study on Mexican *R. mangle*. The discrepancy between the two studies may be due to the small sample size ($n = 12$ vs. 50) and a lack of control over inter- and intra-annual variability of the former study. Although taxonomic differences cannot be excluded, it is clear that a time-standardized measuring approach should be used when comparing wood anatomical features between different sites in any dendroecological investigation. The developmental link between increasing vessel density with salinity can be explained by an adjustment in nutrient availability and/or auxin physiology with higher soil water salinity. Salt stress interferes with the uptake of nutrients such as $Ca^{2+}$, $Mg^{2+}$ and $K^+$ (Popp *et al.*, 1985; Naidoo, 2006; Súarez and Medina, 2006) and is reported to decrease auxin concentrations in poplar, leading to a decrease in vessel size (Junghans *et al.*, 2006). Although vessel density was not evaluated by Junghans *et al.* (2006), a previous study notes that vessel density could also be affected by auxin (Aloni, 2004).

The functional significance of the changes in vessel densities in trunks of *R. mucronata* have also been considered. A high salinity creates an osmotic stress subjecting the xylem vessels to the risk of cavitation and subsequent embolism (Sperry and Tyree, 1988; Tyree and Sperry, 1989; Hacke and Sperry, 2001). The associated increase in vessel density may be interpreted as a strategy for conductive safety. The benefit is offered in two ways. First, when the same number of vessels are cavitated, a higher percentage of the transport system remains functional in wood of high vessel density than in wood of low vessel density (Baas *et al.*, 1983; Villar-Salvador *et al.*, 1997; Mauseth and Plemons-Rodriguez, 1998). Second, because vessels are not linear features (Tyree and Zimmermann, 2002; Kitin *et al.*, 2004), a high proportion of vessels are at least at one point along their length in contact with each other via inter-vessel pits. Therefore, embolized vessels can be circumvented by means of the large number of alternative routes for water transport (Tyree *et al.*, 1994; Carlquist, 2001).

The environmental responsiveness of vessel diameter to soil water salinity was found to be remarkably low, and

therefore its proxy potential is limited. Only a small tendency was shown towards smaller radial diameters at sites with a high salinity and during the dry season (Fig. 4B, Table 3). This does not correspond to the findings of an earlier study on *R. mucronata* from Kenya: a high-resolution time series analysis, but only considering one site, showed that radial as well as tangential diameters were smaller in the dry than in the rainy season (Verheyden *et al.*, 2005). A high-resolution approach might thus be required to reveal minor adjustments in tangential diameter (Tables 2 and 3). Similar to our results, Gillespie *et al.* (1998), during a study on *Breonadia salicina*, a tree of tropical, subtropical and semi-arid areas, also observed radial diameters to be more responsive to rainfall than were tangential diameters. This finding is further supported by the strikingly similar size distributions of the tangential as opposed to the radial diameters at sites with contrasting soil water salinity and inundation frequency (Fig. 5A, B). The authors concluded that radial diameter measurements should not be neglected in favour of tangential diameters, in agreement with the results presented herein.

Aside from a high vessel density, declining vessel dimensions are repeatedly mentioned in association with an increased conductive safety (Lo Gullo *et al.*, 1995; Villagra and Roig Juñent, 1997; Arnold and Mauseth, 1999; Corcuera *et al.*, 2004; Stevenson and Mauseth, 2004). The absence of a clear salinity effect on vessel diameters in this study (Table 2, Fig. 4B) can be explained by one or a combination of the following aspects. First, the discrepancy between tangential and radial diameter does not result from a prospective relationship between radial diameter and growth rate, either within (Table 2, Fig. 3) or between trees ($r^2 = 0.044$, $P$ = n.s., $n = 20$). The growth rate effect on vessel diameters reported by Reich *et al.* (2003) in 17 oak species in Florida may thus be an effect of environmental factors, correlated with growth rate (e.g. salinity). However, the incongruence may simply reflect inter-generic variation. An extensive analysis of the effect of growth rate on wood anatomy is needed to confirm the findings presented here. Secondly, xylem vessels with a bimodal diameter distribution offer the advantage of an efficient (large vessels) and safe (small vessels) water transport system (Mauseth and Stevenson, 2004). The functional benefit of this vessel combination explains its frequent occurrence in the flora of arid regions (Baas *et al.*, 1983; Baas and Schweingruber, 1987; Villagra and Roig Juñent, 1997). However, as in the mangrove *Aegiceras corniculatum* (Sun and Lin, 1997), no bimodal vessel diameter distributions were detected in *R. mucronata* (Fig. 5). A third factor potentially interfering with an ecological trend in vessel diameter is age (Corcuera *et al.*, 2004). In both radial (Verheyden *et al.*, 2005) and tangential diameter (N. Schmitz, unpubl. res.) an age trend has sometimes been observed. To maintain a favourable water balance, when the tree is growing and increasing its leaf surface, trees usually produce longer and wider vessels in their stems with age (Tyree and Ewers, 1991; Hudson *et al.*, 1998; Cruiziat *et al.*, 2002). The vessels in SAL4 and SAL6 are larger than expected if a negative trend with salinity were present, but the impact of age can be excluded. The large vessels in both salinity categories are

represented by young trees with a cambial age of, respectively, 11–24 and 4–20 years while the small vessels of SAL5 occurred in the oldest trees with a cambial age of 25–57 years (Fig. 4B, Table 1). Alternatively, cell wall thickness and thus conduit reinforcement could be more important than vessel lumen area with respect to conductive safety (Hacke and Sperry, 2001; Hacke *et al.*, 2001). The absence of a selective force might then explain the missing plasticity in vessel size. In addition, differences in nutrient availability between the study sites might have interfered with salinity. Lovelock *et al.* (2006) found an increase in vessel diameter in *R. mangle* in response to P addition whereas vessel density did not change to any great degree. Finally, future studies should address the role of pit characteristics in the invariability of vessel diameter with changing salinity conditions. According to the air-seeding hypothesis, tension-induced cavitation is the result of air being sucked in via the pores in the inter-vessel pit membranes (Tyree *et al.*, 1994; Choat *et al.*, 2003; Konrad and Roth-Nebelsick, 2003). The presence of small pit pores in small vessels would provide them with a higher cavitation resistance as compared with large vessels (Tyree and Dixon, 1986; Sperry and Tyree, 1988; Lo Gullo and Salleo, 1991, 1993; Hargrave *et al.*, 1994; Jarbeau *et al.*, 1995). However, the relationship between vessel and pit pore diameter is still a subject of debate. Small pit pore diameters (Tyree *et al.*, 1994; Sperry and Hacke, 2004) and/or small surface area of the intervessel pits (Orians *et al.*, 2004; Wheeler *et al.*, 2005; Ellmore *et al.*, 2006; Hacke *et al.*, 2006) have been reported to increase the cavitation resistance of the water transport system regardless of vessel diameter.

As with vessel diameter, vessel density is independent on both growth rate and age. Together with the clear trend of increased density with salinity, this validates the earlier suggestion of vessel density as a salinity proxy (Verheyden *et al.*, 2005). However, as indicated by the overlap in the data (Fig. 4), application of the findings is restricted to comparative studies and no absolute salinity values can be predicted based on vessel density. The overlap in the data can at least partly be attributed to the interplay between salinity and inundation frequency in their influence on the vascular features of mangrove trees. In addition to a decrease in salinity, a lower inundation class is also observed to result in the presence of relatively few vessels (George and Nielsen, 2000; Woodcock *et al.*, 2000; Yáñez-Espinosa and Terrazas, 2001), as this study confirms (Table 2). Again, no such findings were reported by Yáñez-Espinosa *et al.* (2001) on *R. mangle* from Mexico. The interaction between inundation class and salinity as reported here is a result of evaporation of the soil water when the tide is out, alternating with a regular or only an occasional flooding with sea water at, respectively, low and high inundation classes (Lin and Sternberg, 1992, 1993; Passioura *et al.*, 1992). Aside from differences in tidal regime, the overlap in vessel density data may be caused by other factors that cause salinity to vary within and between sites. As mentioned above, these factors include land run-off, groundwater flow, river input, soil type and the degree of evaporation. In future studies, these factors must be accounted for just as wood anatomical features have to be sought that are exclusively related to salinity or inundation frequency. For example, ray height was found to give a good correlation with inundation frequency in some mangrove species of Mexico (Yáñez-Espinosa *et al.*, 2001). A combination of different wood anatomical features might then result in a proxy that allows the reconstruction of absolute changes in salinity, rather than only relative changes when studying vessel density alone. This proxy will be of intra-annual resolution as the salinity data are integrated over the rainy or dry season.

## CONCLUSIONS AND PERSPECTIVES

In this study, a clear trend of increasing vessel density with increasing soil water salinity was demonstrated. Although more data are required, neither age nor growth rate were found to interfere with the relationship between vessel density and salinity. Vessel density is therefore a promising environmental proxy, in particular for tropical dendrochronology, as adequate proxies for tropical regions are limited (Robertson *et al.*, 2004; Speer *et al.*, 2004; Brienen and Zuidema, 2005; Heinrich and Banks, 2005). Vessel diameter was surprisingly less sensitive to changes in salinity. Radial diameter was slightly more responsive to environmental variations than was tangential diameter; this variation cannot as yet be explained. In *R. mucronata* of Gazi Bay it is therefore a high vessel frequency and not small vessel size that most likely represents a strategy for conductive safety. This study has helped to elucidate the link between the hydraulic architecture of trees and their environment. However, to resolve this research question fully, insight has to be gained into the functional significance of the lack of plasticity in vessel diameter, the link with inter-vessel pits and the underlying developmental and physiological processes.

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