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A safe hydraulic architecture as wood anatomical explanation for the difference in distribution of the mangroves *Avicennia* and *Rhizophora*

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Summary

1. Wood anatomical characteristics are an important source of information about how trees are coping with the conflicting requirements of optimal hydraulic conductivity and safety. In this study we compared the vessel characteristics of *Avicennia marina* and *Rhizophora mucronata* to contribute to a better understanding of the difference in distribution of these two mangrove species.

2. Density, grouping and diameters of vessels together with vessel element length of *A. marina* trees growing on seven different study sites in Gazi Bay (Kenya) were measured and compared with the vessel characteristics of *R. mucronata* of the same research area. Furthermore, the relation of environmental factors related to the water relations of mangrove trees to the wood anatomy of both species was tested.

3. Vessel density of both species and vessel grouping of *A. marina* are higher with higher salinity. In addition, *A. marina* was shown to have a higher vessel density, a higher vessel grouping, smaller vessel diameters and shorter vessel element lengths as compared to *R. mucronata*.

4. As the vessel characteristics of *A. marina* are related to protection against cavitation or the effects of cavitation, we can infer that this species has a water transport system which can be considered safer under water limiting conditions than that of *R. mucronata*.

5. The contrast in the safety of the water transport system between the two mangrove species studied is reflected in their distribution at local scale, over the land-sea ecotone, and it may also explain the wide latitudinal distribution of *A. marina* as compared to *R mucronata*.

6. This conclusion emphasizes the importance of the anatomy of the water transport system for survival under diverse environmental conditions. In general it is shown that dominant species of a single ecosystem can deal with the stressful conditions they live in by contrasting ecological strategies.

Key-words: *Avicennia marina*, ecological wood anatomy, hydraulic safety, inundation, local and global mangrove distribution, *Rhizophora mucronata*, salinity, vessel characteristics

Introduction

Mangrove forests are a characteristic feature of the intertidal zone of tropical and subtropical coasts. As these forests are regularly flooded with seawater, mangrove trees do not only have to cope with high temperature and low relative air humidity but also with high and changing salt concentrations and hypoxia due to regular inundation. In order to survive under these extreme and continuously changing environmental conditions mangrove trees have developed different types of adaptations. Aerial roots, vivipary, salt exclusion and salt secretion are typical though not exclusive characteristics of mangrove trees (Scholander 1968; Popp *et al.* 1993; Tomlinson 1994; Shi *et al.* 2005) that partially explain their presence in this peculiar environment. *Avicennia* L. and *Rhizophora* L., the most characteristic genera of mangrove systems worldwide (Fig. 1), have different solutions to deal with the extreme ecological conditions under which they thrive: *Avicennia* spp. have cable roots with pneumatophores and can exclude and secrete salt, while *Rhizophora* spp. are growing on stilt roots and can exclude but not secrete salt (Tomlinson 1994).

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Fig. 1. *Avicennia marina* (above) and *Rhizophora mucronata* (below) in Gazi Bay, Kenya. *Avicennia* spp. have cable roots with pneumatophores, while *Rhizophora* spp. are growing on stilt roots.

The most limiting factor for trees growing in a saline environment is the risk for cavitation – that is air bubble formation in the xylem sap (Cochard 2006) – blocking water transport. Since cavitation is already highly influencing the functionality of the hydraulic system under mesophilic conditions (e.g. Zimmermann & Brown 1971), the survival of mangrove trees in their extreme environment is even more surprising. Plants, and especially mangroves, face a trade off between the protection of their water transport system against cavitation and conducting capacity (e.g. Mauseth & Stevenson 2004; Hacke *et al.* 2006). High vessel density, high vessel grouping, small vessels and short vessel members have already been mentioned as adaptations to avoid reduction of hydraulic capacity after cavitation and subsequent air-filling of vessels (e.g. Baas *et al.* 1983). But does the high cavitation risk in the mangrove environment lead to a general mangrove hydraulic structure or are there different alternative strategies between mangrove species to deal with the threats for the water transport, in view of their distinctive ecology?

Although *Avicennia* and *Rhizophora* are the two dominant mangrove genera, their geographical distribution is different: the range of *Avicennia* is wider than that of *Rhizophora*, southward as well as northward, in both the Eastern and the Western biogeographic mangrove regions (Duke 1991; Spalding *et al.* 1997). In its habitat preference, *Avicennia* can be observed near the sea as well as in the more inland parts of the mangrove area, while *Rhizophora* only grows at the seaward end of the mangrove forest (MacNae 1963; Duke 1991; Dahdouh-Guebas *et al.* 2004). Mangrove forests near the sea are inundated twice daily by seawater with almost constant salinity levels. This limits the range of salinity seashore trees are exposed to. More land-inward parts of the forests, in contrast, are exposed to a wider range of salinity values due to less frequent inundation and evaporation (Yáñez-Espinosa *et al.* 2001; Naidoo 2006). So *Avicennia* spp., growing in both the border parts of the mangrove forest, must be more eurytopic than *Rhizophora* spp. for salinity and inundation. What are possible explanations for both the co-occurrence and the local and global differential distribution of *Avicennia* spp. and *Rhizophora* spp.? Are there wood anatomical factors at the base of the wider ecological success of *Avicennia* spp.?

Stuart *et al.* (2007) addressed the role of freezing in the distributions of mangrove trees, but information about the underlying factors of the ecological success and wider distribution of *Avicennia* spp. as compared to *Rhizophora* spp. remains scarce. Vessel anatomy can tell how plants are dealing with the conflicting interests of safety and efficiency. As this balance on its turn is of high importance in where trees can grow, studying the vessel anatomy of mangrove trees can help to clarify mangrove distribution ranges. In the present article, we addressed the question of the ecological significance of wood anatomical features by the study of the hydraulic architecture of *Avicennia marina* (Forssk.) Vierh. and *Rhizophora mucronata* Lamk. from Gazi Bay (Kenya). The objectives were (i) to document the differences in vessel characteristics (vessel density, vessel grouping, vessel diameters and vessel element length) between both species and (ii) to explain the difference in local distribution of both species by these differences in characteristics of the water transport system. The hypothesis is that *A. marina* has a wider local distribution as compared to *R. mucronata* due to a water transport system that is better adapted to a broad range in environmental conditions.

Materials and methods

STUDY AREA

The research was conducted in the mangrove forest of Gazi Bay (4°25′ S, 39°30′ E) situated at the east coast of Kenya (Fig. 2), at about 50 km south of Mombasa. The forest covers an area of about 600 ha (UNEP 2001; Neukermans *et al.* 2008) and is dominated by *R. mucronata*, *A. marina* and *Ceriops tagal* (Matthijs *et al.* 1999; Dahdouh-Guebas *et al.* 2004). The climate of the area is tropical, with a bimodal precipitation distribution: a distinct dry season (December–March) is followed by a long rainy season (April–July) and another short rainy season (October–November). Mean annual temperatures range from 22 to 30 °C, while mean relative humidity varies between 65% to 81% (annual averages of minima and maxima for Mombasa for the period 1972–2001, data from the Kenyan Meterological Department, Mombasa, Kenya). During the wet season, the Mkurumuji and the Kidogoweni, two seasonal rivers (Fig. 2), are important sources of freshwater for the surrounding mangrove forests (Kitheka, 1997).

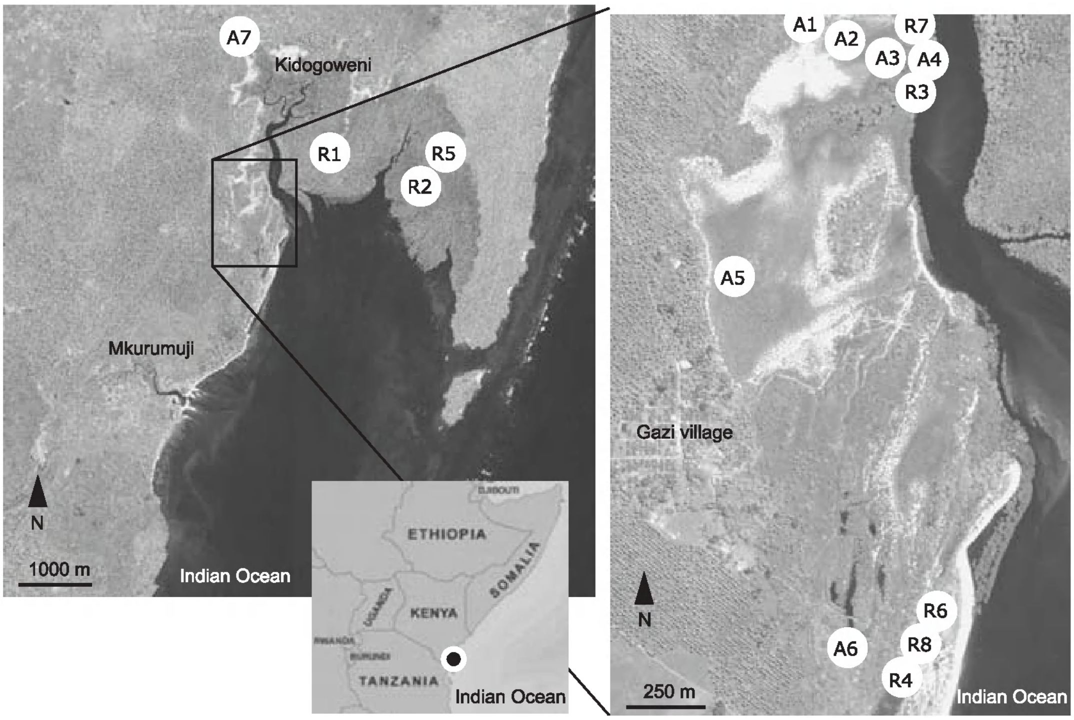

Fig. 2. QuickBird satellite image of Gazi Bay acquired in 2002 (Neukermans *et al.* 2008) and map of east Africa situating Gazi Bay on the Kenyan east coast (black dot). The seven study sites where stem discs of *Avicennia marina* were taken are indicated (A1–A7) together with the eight study sites of *Rhizophora mucronata* (R1–R8) (Schmitz *et al.* 2006). The Mkurumuji and the Kidogoweni, two seasonal rivers that provide freshwater to the mangrove forest in Gazi Bay, are indicated on the left satellite image.

SAMPLE COLLECTION AND PREPARATION

Wood discs of 35 *A. marina* trees were collected in June 2006. Before sampling, tree height of each tree was determined trigonometrically and stem diameter at the base of the tree was measured. The samples, with a diameter range of 2–7 cm, were all taken at a height of 1·3 m and originate from trees growing in seven different sites (five samples per site) (A1–A7, Fig. 2). The sites were selected for their difference in environmental conditions. All wood samples are now part of the collection of the Royal Museum for Central Africa in Tervuren (Belgium) as are the samples of *R. mucronata* already collected in 1999 and 2002 in eight different study sites (R1–R8, Fig. 2) (Schmitz *et al.*, 2006). Wood samples were air-dried and sanded using a series of sandpaper from 100 to 1200 grit.

WOOD CHARACTERISTICS

Vessel features were measured on the sanded stem discs of *A. marina* under optical magnification of 12·5 times using digital image analysis software (AnalySIS Pro version 3·2, Soft Imaging System GmbH, Münster, Germany). On every sample in the two or three outermost growth segments, that is units of xylem and phloem originating from the same cambium, the radial and tangential diameter of at least 190 vessels as well as the xylem and phloem surface area of the growth segments were measured. For each number of vessels grouped together, the amount of vessel groups was counted. From these data we calculated the vessel density (number of vessels per mm^2), the proportion of phloem to xylem, the percentage of solitary vessels for each segment (number of solitary vessels per total number of vessels), the vessel grouping index (mean number of vessels per vessel group), the vessel surface area of each vessel and the ratio of radial to tangential diameter per vessel. For comparison with *R. mucronata* we used vessel density and vessel diameter data from our earlier study (Schmitz *et al.* 2006). Data for vessel grouping in *R. mucronata* were obtained by counting the amount of vessel groups for each number of grouped vessels in the same measuring fields as used in Schmitz *et al.* (2006).

Vessel element length of *A. marina* and *R. mucronata* from nine trees out of three study sites for each species (A3, A4, A6, R3, R5 and R7, Fig. 2 – three trees per study site) was studied after maceration with hydrogen peroxide and acetic acid. A minimum of hundred vessel elements per tree was measured at an optical magnification of fifty times using digital image analysis software (as above). The vessel element length was measured from perforation plate to perforation plate, tails not included. Wood samples for maceration were taken at 1 cm from the pith on wood discs taken at 1·4 m height.

SITE VARIABLES

For all 14 sites, height above datum was calculated using tracing and local tide tables. Inundation classes were then calculated according to Tomlinson (1994). Inundation classes I, II, III and IV are attributed to sites inundated by respectively 100–76%, 75–51%, 50–26%, 25–5% of the high tides. One to three salinity measurements of the soil water of each study site were conducted between 1998 and 2007 by use of a WTW P4 multiline conductivity meter or a hand-held refractometer, as described in Schmitz *et al.* (2006, 2008b). Hemispherical images were taken at nine sites (A1–A7, R3, R8, Fig. 2) to calculate the Leaf Area Index integrated over 0–75° with the software programme *Gap Light Analyser version 2·0* (Simon Fraser University, British Columbia and the Institute of Ecosystem Studies, New York). Soil texture was

Table 1. Wood anatomical description of the water transport system of *Avicennia marina* and *Rhizophora mucronata* based on the measurements for all trees from all study sites (A1–A7 and R1–R8, see Fig. 2)

	Median	Q1	Q3	Minimum	Maximum	*n*
Avicennia marina						
Vessel density – xylem (number of vessels mm^{-2} xylem area)	78·68	66·12	98·25	26·88	147·67	82
Vessel density – xylem + phloem (number of vessels mm^{-2} stems area)	57·95	46·49	70·73	17·38	110·82	82
Phloem : xylem ratio	0·38	0·31	0·43	0·22	0·63	82
Solitary vessels (%)	28·78	20·99	38·78	3·22	57·55	82
Vessel grouping index*	4·07	3·73	4·58	3·17	6·62	82
Radial diameter (μm)	36·47	23·74	51·67	5·78	115·50	8692
Tangential diameter (μm)	39·00	26·24	52·48	5·57	107·87	8692
Radial diameter : tangential diameter ratio	0·96	0·80	1·14	0·27	3·75	8692
Vessel surface area (μm^2)	1085·74	501·11	2043·41	37·94	8463·18	8692
Vessel element length (μm)	186·22	147·32	221·66	33·89	380·47	1127
Rhizophora mucronata						
Vessel density – xylem (number of vessels mm^{-2} xylem area)	25·65	21·51	32·34	12·51	66·02	279
% solitary vessels	78·57	71·05	83·78	42·11	100·00	279
Vessel grouping index*	1·26	1·18	1·36	1·00	1·80	279
Radial diameter (μm)	79·89	71·63	90·91	24·79	134·99	7447
Tangential diameter (μm)	71·63	63·36	77·13	24·79	115·70	7513
Vessel element length (μm)	682·51	593·02	781·65	285·04	1171·25	900

*Mean number of vessels per vessel group; Q1, lower quartile; Q3, upper quartile; *n*, total number of measurements.

determined for eight sites (A1–A7, R3, Fig. 2) by standard field characterization methods (GLOBE, 2005). Nutrient concentrations (NO_3^-, NH_4^+ and soluble reactive P) were measured by standard procedures (APHA-AWWA-WEF 1995) from water samples taken 1 day after spring tide in February 2007 at the seven *A. marina* sites.

STATISTICAL ANALYSIS

The non-normal distribution of categorised (by study site) wood characteristics of *A. marina* did not allow for parametric tests, so Kruskal–Wallis tests were carried out for each variable (vessel density, proportion of phloem to xylem, vessel grouping index, radial diameter, tangential diameter, ratio of radial to tangential diameter, vessel surface area and vessel element length) with each factor (mean salinity, maximum salinity, minimum salinity, salinity range, inundation, mean NO_3^- concentration, mean soluble reactive P concentration, Leaf Area Index, tree height, stem diameter at 1·3 m and stem diameter at the tree base) with the exception of the mean NH_4^+ concentration for which the data set was considered insufficient. For *R. mucronata* Kruskal–Wallis tests for vessel density, vessel grouping, radial and tangential diameter and vessel element length were conducted for mean salinity, inundation, tree height, stem diameter at 1·3 m and stem diameter at the tree base. Mann–Whitney U tests were done to test for significance of differences in non-normal distributed wood characteristics between groups of *A. marina* study sites. In order to evaluate if the site effect is considerable (variation between the study sites is bigger than the variation within the study sites) variability plots were made for all wood characteristics of both species. All statistical analyses were conducted using STATISTICA 7·0 (StatSoft Inc., Tulsa, OK).

Results

A wood anatomical description of *A. marina* and *R. mucronata* can be found in Table 1. An overview of the collected environmental data can be found in Schmitz *et al.* (2008b) and in Table S1 of the Supporting Information. All environmental factors tested had a significant effect on the wood variables of *A. marina* and *R. mucronata* – P-values of Kruskal–Wallis tests at least lower than 0·05 but often lower than 0·001 – in contrast to the non-systematic effect of tree factors on the wood variables – Kruskal–Wallis tests often non-significant (see Tables S2 and S3 in Supporting Information).

Variability plots of vessel density and vessel grouping showed a considerable site effect in both *A. marina* and *R. mucronata*. There was a significant difference in vessel density of *A. marina* between the study sites with a mean salinity below 51·0‰ and above 57·6‰ ($U = 347{\cdot}00$, $P < 0{\cdot}001$, Mann–Whitney U test, Fig. 3), a minimum salinity below 20·9‰ and above 38·0‰ ($U = 347{\cdot}00$, $P < 0{\cdot}001$, Mann–Whitney U test) and a maximum salinity below 68·2‰ and above 70·0‰ ($U = 270{\cdot}00$, $P < 0{\cdot}001$, Mann–Whitney U test), the latter with exception of the study site with a maximum salinity of 90·0‰. In all three cases higher vessel density was found in sites with higher salinity values. Furthermore the vessel grouping index of *A. marina* in the two study sites with the highest mean salinity values were significantly higher than this of the study sites with a mean salinity equal to or lower than 63·3‰ ($U = 352{\cdot}00$, $P < 0{\cdot}001$, Mann–Whitney U test, Fig. 4). Increasing vessel density with increasing salinity was also found in *R. mucronata* (also see Schmitz *et al.* 2006), vessel grouping however was not higher in sites with higher mean salinity.

In spite of a high variability in radial and tangential diameter in *Avicennia* trees of the same study site, a study site effect can still be observed. Although the smallest radial diameters and the smallest vessel surface areas can be found in the study sites

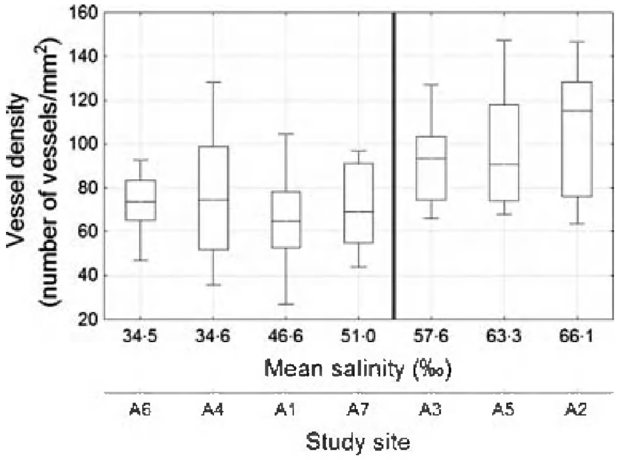

Fig. 3. Median of the vessel density in relation to mean salinity for *Avicennia marina*. Each salinity value represents one study site. The vertical line separates a group of lower vessel densities from one of higher vessel densities ($U = 347{\cdot}00$, $P < 0{\cdot}001$, Mann–Whitney *U* test). line (median), box (25–75%), whiskers (non-outlier range).

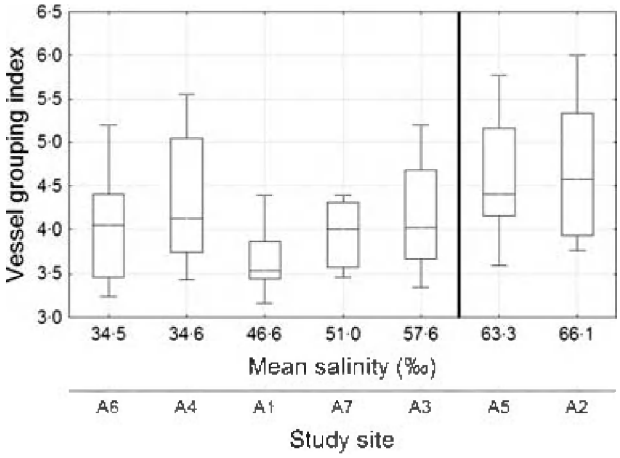

Fig. 4. Median of the vessel grouping index (mean number of vessels per vessel group) in relation to mean salinity for *Avicennia marina*. Each salinity value represents one study site. The vertical line separates a group of lower vessel grouping from one of higher vessel grouping ($U = 352{\cdot}00$, $P < 0{\cdot}001$, Mann–Whitney *U* test). line (median), box (25–75%), whiskers (non-outlier range).

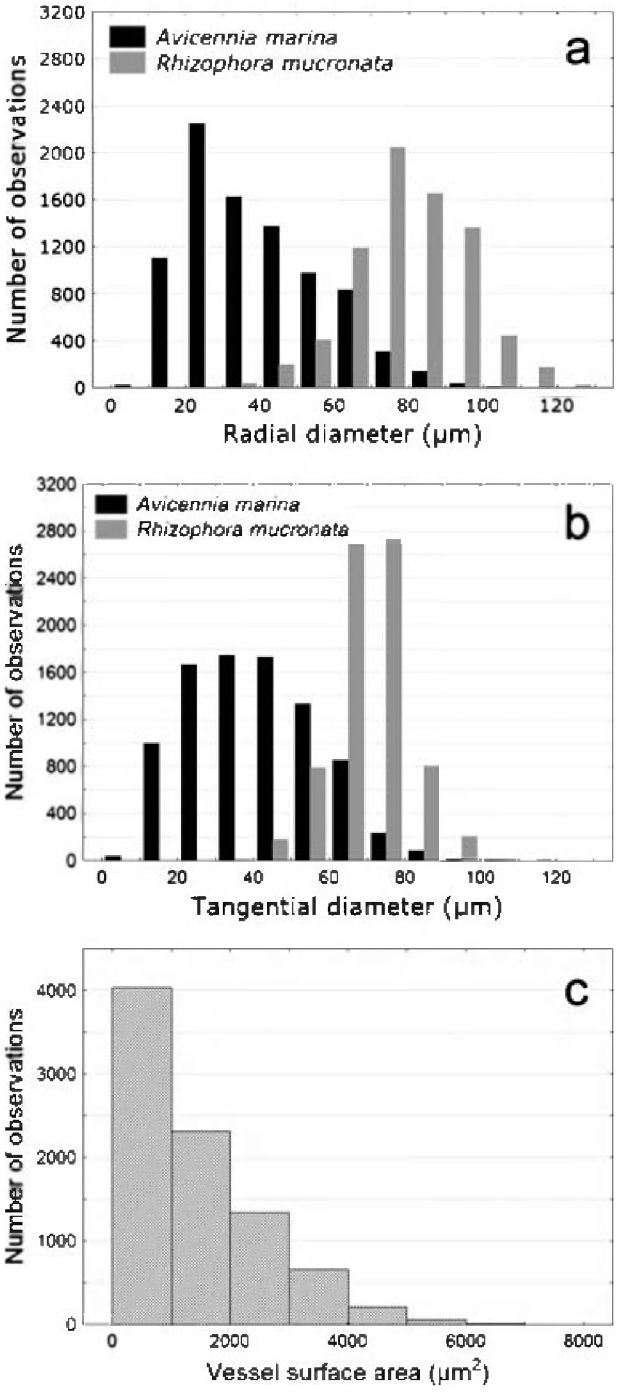

Fig. 5. Frequency distribution of the radial (a) and tangential (b) diameters in *Avicennia marina* and *Rhizophora mucronata* and of vessel area in *A. marina* (c).

with the highest mean salinity, vessel diameters varied little with mean salinity in *A. marina*. Frequency distributions of vessel dimensions in *A. marina* show a definite right skewed curve for radial vessel diameter (Fig. 5a) and vessel surface area (Fig. 5c) and a less pronounced right skewed distribution for tangential diameter (Fig. 5b). In *R. mucronata* on the contrary radial (Fig. 5a) as well as tangential diameters (Fig. 5b) have tendency to the normal distribution. The ratio of radial to tangential diameter in *A. marina* is close (Table 1) and highly centred to one, meaning that most vessels in this species are nearly circular.

Discussion

STRATEGIES OF MANGROVE TREES TO SURVIVE

All environmental factors tested had a significant effect on the wood anatomy of *A. marina* in Gazi Bay, but only salinity gave rise to visually observable trends in different vessel characteristics. The same direct and important relationship between salinity and wood anatomy is reported for *R. mucronata* (Schmitz *et al.* 2006) and also growth layer width in *A. marina* is depending on salinity conditions (Schmitz *et al.* 2008b). In this regard, it can be concluded that salinity is the dominant factor of impact on the wood anatomy of mangroves, and this on tissue as well as on cellular level.

Vessel density and not vessel dimension is found to be the most responsive wood characteristic to varying salinity conditions in both *A. marina* and *R. mucronata*. The osmotic stress due to high salinity causes low water potential (causing a high tension or negative pressure) in the xylem sap of mangrove species (Scholander *et al.* 1965; Scholander 1968). This tension on turn causes a higher probability for cavitation events (Tyree & Sperry 1989; Hacke & Sperry 2001; Naidoo 2006). Even though vessel diameters are found to be smaller in various tree species under more stressful conditions for the water transport (Lo Gullo *et al.* 1995; Villagra & Juñent 1997; Corcuera *et al.* 2004; Choat *et al.* 2005), these two mangrove species seem to deal with the higher cavitation risk at higher salinity values mainly by an increased vessel density. The same trend has been observed in the mangrove *Laguncularia racemosa* in Mexico (Yáñez-Espinosa *et al.* 2004). Furthermore, Melcher *et al.* (2001) found that *Rhizophora mangle* trees growing at sites of higher soil water salinity were more vulnerable to cavitation then those from sites with lower salinity levels. So the mechanism of higher vessel density under physiological conditions with higher cavitation risk via a gradual density increase in *R. mucronata* (Schmitz *et al.* 2006) and an abrupt increase around a salinity of 55‰ in *A. marina* (Fig. 3), is present in phylogenetically distant mangrove species (Schwarzbach & Ricklefs 2001; Shi *et al.* 2005). As Dahdouh-Guebas *et al.* (2004) indicated a genetic difference between landward and seaward *A. marina* stands in Gazi Bay, we cannot confirm whether either plasticity within a genotype or adaptive variation among genotypes is contributing more to the differences in vessel density between the different study sites. Despite the uncertainty about its underlying cause, a higher vessel density under more saline conditions can be considered a common mechanism in trees in the mangrove ecosystem in order to deal with the severe and dynamic conditions of their environment. These results are reinforcing the findings of Verheyden *et al.* (2005) who discovered a within-tree variation in the vessel density of *R. mucronata* depending on the growth season.

Although vessel density reflects the overall salinity of the site, the maximum salinity of study site A1 (Fig. 2) is not reflected in a high vessel density in *A. marina*. The soil water salinity of this most land inward site of *A. marina* has an extremely high maximum salinity due to a low inundation frequency – only a few days of flooding a month – together with high evaporation during the dry season (Naidoo 2006). But during the rainy season high amounts of intermittent freshwater run-off leads to a serious decline in soil water salinity. This rather low salinity after periods of rain most probably compensates for the high cavitation risk during drier periods leading to trees that have a much lower vessel density than expected. A high vessel density optimizes the water transport under stressful conditions by allowing a more efficient bypass of air-filled vessels and by leaving more vessels functional for the same number of embolized vessels, as was already suggested by Schmitz *et al.* (2006). In non-stressful conditions such as high freshwater availability, this safety solution is however unnecessary and weighed against more advantageous characteristics of the vessel network.

It is remarkable that the vessel density of trees from the same species growing in one forest, so on a very small geographical scale, is different according to differences in environmental conditions. Moreover, this vascular trait variation happens in a parallel way in the two main species of the mangrove ecosystem. Vessel characteristics, especially adaptively-changing vessel densities, only partially explain how mangrove trees survive in their environment. Intervessel pit characteristics also appear to play a role in safeguarding the water transport in the dynamic mangrove environment (Lopez-Portillo *et al.* 2005; Schmitz *et al.* 2007; Schmitz *et al.* 2008a). We are however far from understanding the full spectrum of the mangrove anatomy and functioning in relation to the mangrove environment. But what can the wood anatomy of *A. marina* and *R. mucronata* throw in to the explanation of the ecological distribution and the biogeography of these mangrove species?

AVICENNIA: THE SAFER ONE

From the comparison between *A. marina* and *R. mucronata* based on all vessel characteristics studied (Table 1) can be inferred that the water transport systems of both species are highly different. This is also true in the study site where both species grow together (A4 and R3, Fig. 2, Table 2). Former studies on wood characteristics in *R. mucronata* have already proven the plasticity potential of vessel density and radial vessel diameter in this species (Verheyden *et al.* 2005; Schmitz *et al.* 2006). Furthermore, the present study and other studies on different mangrove species (e.g. Sun & Suzuki 2000; Yáñez-Espinosa *et al.* 2001; Sobrado 2007) provide additional evidence for adaptation of hydraulic characteristics to the environment mangrove trees live in. However, one should be aware that also the different genetic background of the species could be expressed in their hydraulic structure. Yet even when the phenotypic plasticity of the studied wood characteristics turns out to be low, the highly different structure of both species living in the same habitat can have a major effect on the tolerance towards environmental factors, thus defining the species distribution.

In *A. marina* we observed a dominance of smaller vessel diameters, in contrast to *R. mucronata* where vessels of intermediate size were more frequent (Fig. 5). Although a link between vessel diameter and cavitation sensitivity is not generally accepted, other studies show (species with) smaller vessels to be less prone to cavitation (Lo Gullo & Salleo 1991; Hargrave *et al.* 1994; Lo Gullo *et al.* 1995; Choat *et al.* 2003). As *A. marina* not only has smaller vessels than *R. mucronata* but also has a larger proportion of the tiniest vessels, a link between small vessel diameter and low vulnerability to cavitation would include that the water transport system of

Table 2. Comparison of the wood anatomical characteristics of *Avicennia marina* and *Rhizophora mucronata* at a study site where both species grow together (A4 and R3, see Fig. 2)

	A. marina				*R. mucronata*			
	Median	Q1	Q3	*n*	Median	Q1	Q3	*n*
Vessel density – xylem (number of vessels mm^{-2} xylem area)	74·44	51·70	98·73	11	22·85	20·02	26·14	24
Solitary vessels (%)	31·73	17·28	44·33	11	78·66	71·39	86·10	24
Vessel grouping index*	4·13	3·74	5·05	11	1·26	1·17	1·33	24
Radial diameter (μm)	38·58	23·74	57·07	1192	79·89	71·63	88·15	485
Tangential diameter (μm)	42·98	28·65	58·30	1192	68·87	63·36	74·38	480
Vessel element length (μm)	172·21	132·43	205·97	360	719·94	638·60	769·24	300

*Mean number of vessels per vessel group; Q1, lower quartile; Q3, upper quartile; *n*, total number of measurements.

A. marina is double safe. Intervessel pit characteristics are however supposed to explain differences in vulnerability to cavitation better than vessel diameters (Jarbeau *et al.* 1995; Hacke & Sperry 2001; Wheeler *et al.* 2005; Hacke *et al.* 2006; Choat *et al.* 2008). A safety difference between *A. marina* and *R. mucronata* is found in the morphology of their intervessel pits. Schmitz *et al.* (2007) observed that several pit characteristics in *A. marina* – smaller pitfield fractions, smaller inner and outer pit apertures, smaller individual pit size, thicker pit membranes and the presence of vestures – could be linked to a safer water transport system if compared to *R. mucronata*.

Avicennia marina does not only have small but also nearly circular vessel areas (Table 1). Observations of more circular vessels in different *Rhizophora* species growing on locations with lower annual rainfall and longer dry seasons (Nele Schmitz, unpublished data) and in *Aesculus hippocastanum* growing on sites with high salt concentrations due to de-icing salts (Eckstein *et al.* 1976) give a clear indication that more circular vessels offer an additional advantage in stressful conditions, though further data would be needed to explain this observation.

Vessel grouping and vessel density, other important xylem characteristics, are also found to differ between *A. marina* and *R. mucronata* with the vessels of the latter being much less grouped and less dense. Within *A. marina* vessel grouping, as vessel density, is higher in conditions of higher salinity (Fig. 4). High vessel density does not only increase hydraulic efficiency, it also safeguards the water transport system as, compared to a less dense vessel network, a larger proportion of vessel stay functional for the same number of vessels embolized (Baas *et al.* 1983; Mauseth & PlemonsRodriguez 1997; Villar-Salvador *et al.* 1997). High vessel grouping, more probable with high vessel density, can also bring a functional advantage because it allows water to bypass air-filled vessels by alternative pathways created by the intervessel pits of touching vessels in a vessel group (Baas *et al.* 1983; Zimmermann 1983; Yáñez-Espinosa *et al.* 2001; Lopez *et al.* 2005). On the contrary, a higher vessel grouping can also increase cavitation probability as vessel contact, influencing the spread of embolisms, is more intense (Wheeler *et al.* 2005; Hacke *et al.* 2006; Choat *et al.* 2008). We, however, do not know whether either the safety aspect or the cavitation spread is the more important. As we observed higher vessel grouping in more stressful conditions and lower pit field fractions in *A. marina* (Schmitz *et al.* 2007), both safety and cavitation spread are maybe balanced, giving *A. marina* a functional advantage.

Apart from vessel diameter, vessel shape, vessel grouping and vessel density also vessel element length is different between the two species studied: *A. marina* has much shorter vessel elements than *R. mucronata* (Table 1). Furthermore, a preliminary study in different sites showed significantly shorter vessel elements in the higher parts of *R. mucronata* trees, where pressures get more negative (Scholander *et al.* 1965), compared to longer vessel elements at breast height (Elisabeth Robert, unpublished data, $U = 28226{\cdot}00$, $P < 0{\cdot}001$, Mann–Whitney U test). Although vessel length and not vessel element length is generally considered the more important hydraulic characteristic (Baas 1986), further research has to be conducted to find out if smaller vessel elements (i) hinder the spreading of embolisms by their perforation plates and hence are a functional advantage, (ii) are, on the contrary, a functional disadvantage by increasing embolism spread due to higher resistance to xylem sap flow (Ellerby & Ennos 1998; Schulte 1999) and thus larger pressure differences across intervessel pits, or (iii) do not have a functional significance.

Although validation is needed, the interpretation of all wood anatomical characteristics studied does not contradict the following statement: the water transport system of *A. marina* is most probably safer than that of *R. mucronata*. In that respect the ecological success of *A. marina* can be related to the characteristics of its water transport system. As this safety of the water transport is reflected in the local distribution of the mangrove species studied (Fig. 6), we can conclude that the vessel characteristics of *A. marina* and *R. mucronata* explain at least partially the local distribution of both species.

Not only locally but also globally *A. marina* has a wider distribution than *R. mucronata* (Spalding *et al.* 1997). We could therefore expect that the highly different vessel anatomy of these two mangrove species can also contribute to the explanation of their distribution in the Eastern biogeographical mangrove region. Parallel to the ecotone of environmental conditions from sea to land we can expect a transect of environmental conditions that are less and less suitable for

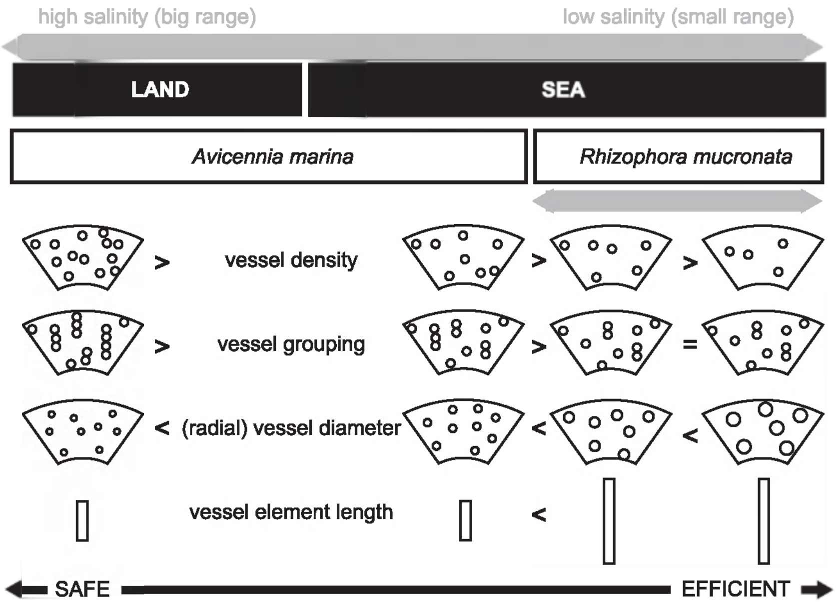

Fig. 6. Overview of the observed wood anatomical characteristics of *Avicennia marina* and *Rhizophora mucronata* trees in function of the location in the mangrove forest. Trees growing more landward, under environmental conditions that are more challenging for the water transport system, such as high salinity and low inundation, are characterised by a water transport system composed of high vessel density, high vessel grouping, small vessel diameters and short vessel elements. Taking the functional interpretation of all these wood anatomical characteristics together, the water transport system of trees at this side of the mangrove forest is considered safer. On the other hand, trees growing on the seashore seem to have a more efficient water transport system, rather lacking adaptations to avoid air in the water column. Arrows are showing ecological gradients (grey) and a gradient from safe to efficient water transport systems (black).

mangrove species from the equator to higher latitude, both north and south. *A. marina* with its safer water transport system could support conditions in which *R. mucronata* cannot survive anymore, logically leading to a more southward and more northward expanded distribution. Moreover the same difference in distribution between *Avicennia* and *Rhizophora* can be observed in the Western biogeographical mangrove region (Spalding *et al.* 1997). We expect that the same results found for *A. marina* and *R. mucronata* can be found for *Avicennia germinans* and *R. mangle*, the most important species of this biogeographical region. Supposing a general difference in wood anatomy between the two mangrove genera studied, the safety of the water transport system of mangrove trees has a high potential to explain the global distribution of mangrove genera at least partially.

We can conclude that the water transport system of *A. marina* in Gazi Bay (Kenya), built of a high vessel density, a high vessel grouping, small vessel diameters and short vessel elements, is contrasting with the water transport system of *R. mucronata* and is expected to be safer based on a physiological interpretation of the combination of observed vessel characteristics. This contrast is reflected in the local distribution of the species and most likely contributes to the explanation of the global distribution of *Avicennia* and *Rhizophora*. Because vessel characteristics are only part of the tree system, patterns in other anatomical and functional factors have to be studied to complete these results. Furthermore, we hypothesize other mangrove species in other localities, in the Eastern as well as in the Western biogeographical mangrove regions, to reflect the same trends, though this still has to be investigated.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Stand characteristics of the study sites in Gazi Bay, Kenya

Table S2. Results of Kruskal–Wallis tests for *Avicennia marina*

Table S3. Results of Kruskal–Wallis tests for *Rhizophora mucronata*