

Hydraulic conductivity and xylem structure of partially buried mangrove tree species

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Abstract

Aims Natural sedimentation rates may not affect mangrove trees adversely, but large and sometimes episodic delivery of sediment may result in decreased growth, dieback or mortality. In this study, we aim to assess the effects of different levels of partial sediment burial on mangrove tree structure and function.

Methods Trees of *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata* were experimentally buried with terrestrial sediment to simulate different sedimentation levels (15, 30 and 45 cm). After 14 months, branch hydraulic conductivity, xylem structure and stomatal properties were assessed.

Results Sedimentation resulted in general increase in hydraulic conductivity following intermediate levels of burial. The process is also associated with varied

anatomical modification in vessel grouping, vessel lumen size and potential conductive area in the three investigated mangrove tree species. Additionally, stomatal adjustment was observed in *C. tagal* with up to 37% reduction of total stomata area in leaves of buried trees.

Conclusions Although sedimentation may stimulate modification in vessel and stomatal properties of buried mangrove trees after a relatively short period of exposure, these traits may not necessarily be important in ensuring hydraulic conductivity which either increases or remains the same as in control following burial.

Keywords Sedimentation · Hydraulic conductivity · Vessel characteristics · Stomata · Mangrove trees · Climate change

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Introduction

Water availability to plants may be a function of many factors including but not limited to, drought, frost, flooding and soil characteristics (texture and structure) as well as salinity as in the case of mangroves (Coder 2000; Stuart 2003; Ball 1988; McDowell et al. 2008; Swift et al. 2008). Sedimentation in mangrove forests may also result in low water availability triggered by increased difficulty in root water absorption (Tomlinson 1994). This may be due to increased soil compaction, which reduces sediment pore sizes and thereby requiring greater tension for water extraction (Sperry et al. 1998). Additionally, sedimentation may lead to increased hypoxia in the sediment (Thrush et al. 2004), and consequently increased physiological drought as water channel proteins (aquaporins) are downregulated by hypoxia (Laur and Hacke 2014) and as such may equally result in decreased water uptake by the roots (Herrera 2013).

The impacts of decreased water uptake as a result of sedimentation can also be equated to physiological drought which may lead to occurrence and propagation of embolism among functional vessels due to increased negative xylem sap pressure above critical threshold (Lens et al. 2013). Most plants experience xylem pressures that are close to the threshold for xylem cavitation (Tyree and Sperry 1988; Lens et al. 2013), cavitation may nevertheless occur merely due to atmospheric moisture fluctuations resulting from transpiration-induced loss of equilibrium within a time scale of a day (Meinzer et al. 2009). However, extreme conditions such as low water availability have been implicated in most literature as the major cause of loss of conductive area in trees (e.g. Ball et al. 2006; McDowell et al. 2008; Awad et al. 2010).

In response to reduced water uptake capacity, plants may display a trade-off between xylem characteristics that ensure safety against cavitation and efficiency in sapflow (de Silva et al. 2012). Amidst controversies, there is at least proof that there is no tree with both high efficiency and safety, though a low of both is quite a common phenomenon (Gleason et al. 2016). For instance, tree species growing in xeric environments tend to show higher vessel grouping as compared to those under mesic conditions (Carlquist 1984). This trait has been found to be one of the most informative in explaining interspecific variation in 50% loss of conductivity, P_{50} (Scholz et al. 2013). In mangroves

growing under highly saline conditions (e.g with salinity range of 50‰ during dry season), the trees form relatively narrower conduits that are often more clustered and are of higher density (Robert et al. 2009a; Schmitz et al. 2006). Leaves can also contribute to minimise hydraulic failure by regulating transpiration rates (Meinzer and Grantz 1990; Wang et al. 1992) through regulation of stomatal conductance to prevent critically negative xylem pressure (Tyree and Sperry 1988; Meinzer and Grantz 1990; Jones and Sutherland 1991).

The current study investigates the influence of increased sedimentation on hydraulic conductivity, xylem structure and stomatal properties of three mangrove tree species (*Avicennia marina* (FORSSK.) VIERH, *Ceriops tagal* (PERR.) C.B. ROB and *Rhizophora mucronata* LAM.), commonly found along the Kenyan coast and generally in the Indo-West Pacific region (Tomlinson 1994). Although sedimentation in mangroves is a natural process facilitated by the aerial rooting structures of the trees (Alongi 2009; Kimeli 2013), only small levels (up to 1.5 cm) of sediment is deposited per annum (Hutchings and Saenger 1987). Large sediment loads may be brought in to this ecosystem associated with anthropogenic activities and increased flooding due to climate change related activities (Bamroongrugsra and Yuanlaie 1995; Caldeira 2012). The study simulates the occurrence of large delivery of sediment in an experimental set-up in plantations. It was hypothesised that such large sedimentation events, (i) lead to increased hypoxia in sediment, (ii) reduced hydraulic conductivity in partially buried trees and (iii) initiated development of adaptive features in stomatal properties and xylem characteristics upon burial. This study provides insight on the ability of mangrove trees to cope with large sedimentation events within their habitat and hence contribute to the assessment of resilience of these forests to various forms of disturbance.

Materials and methods

Study site and experimental set-up

The field experiment was set up in plantations of *C. tagal*, *R. mucronata* and *A. marina* planted in 1994, 1998 and 2001 respectively in Gazi Bay, Kenya (4°25'S, 39°30'E). The bay is situated approximately 50 km south of Mombasa and covers an area of 1800 ha with a mangrove forest coverage of 615 ha (Neukermans

et al. 2008). There are no major developments around the bay except for the three sparsely populated villages of Gazi, Makongeni and Kinondo (Fig. 1a).

The field set-up involved experimental plots that mimic a scenario of three different levels of large sedimentation events in a mangrove forest. Square plots of 2 m by 2 m were selected within the plantations and randomly assigned to the treatments purposely avoiding trees on the outermost edge of the plantations. A set of four plots were selected per species except for *C. tagal* where the area of the plantation was large enough to accommodate two sets, one set closer to the plantation edge and another set of four located about 20 m from the margin of the forest. For the purpose of this experiment the former is referred to as landward and the latter as seaward (Fig. 1a). The selected plots were surrounded with a netting material of 0.5 mm mesh size fixed at a depth of 10 cm below the soil surface and constrained to the ground using wooden pegs to avoid flushing out of sediment from the enclosure. Enclosures were then filled with terrestrial sediment (mainly sandy loam) from adjacent upstream and terrestrial areas to levels of 15 cm, 30 cm and 45 cm excluding the control, where no sediment was added, but the same net and pegs were used (Okello et al. 2014). The establishment of the plots was done in 2010 (*C. tagal*) and 2011 (*A. marina* and *R. mucronata*), and all plots were left to undergo full influence of natural mangrove processes (litter accumulation, natural regeneration and tidal influence). Each tree selected per plot was considered as a replicate of the other as sampling was done within each treatment on different trees.

Structural attributes

Each plot had a varying number of trees that were 1.1 to 4.7 m high (Supplementary Table 1). Stem diameter for *A. marina* and *C. tagal* species was measured at 30 cm ($D_{30\text{cm}}$) since the trees were shorter and could not allow for the conventional diameter measurement at 130 cm (diameter at breast height or $D_{130\text{cm}}$ sensu Brokaw and Thompson 2000). For *R. mucronata*, diameter at breast height or 30 cm above the highest prop root was taken. The diameter range was 1.4–2.1 cm in *A. marina*, 4.0–6.3 cm in *C. tagal* and 11.4–15.5 cm in *R. mucronata* (Supplementary Table 1). Height and diameter measurements were done before subjecting the trees to partial burial. The applied sediment covered the aerial roots to different extents among the studied species, with a

complete coverage in all burial treatments for *C. tagal* (Supplementary Table 1).

Environmental variables

Environmental variables including salinity, sediment nutrient and moisture content, height above datum and redox potential were measured three months after setting up the experiment. Repeated salinity measurements were made monthly for another three months and redox potential was redone after six months. Interstitial water was collected using a punctured plastic tube connected to a vacuum pump and salinity measurements were done with a hand-held refractometer (ATAGO, Tokyo, Japan). Redox measurements were done using a portable oxidation/redox potential (pH/ORP) meter with Automatic Temperature Compensation (ATC) and hold feature (HI 8424, Hanna instruments, USA). For both salinity and soil redox potentials, measurements were done by coring to a depth of 5 cm, thereafter every 10 cm up to 10 cm mark below the original sediment level in each of the treatments, the data was then averaged. Sediment nutrient analysis was done for three sediment cores collected up to 30 cm depth from terrestrial source and in the control plots using standard procedures described by Parsons (1984) and Johnstone and Preston (1993). Soil porosity was determined from moisture content following PUMPSEA (2005) also described in Okello et al. (2014).

Hydraulic conductivity measurements

For the measurements of hydraulic conductivity, three branch samples from three trees of each experimental plot (one branch per tree; 16 plots; $n = 48$) were collected after 14 months of exposure. Only trees that experienced minimal edge effect were considered for sampling. While the choice of branches was random, deliberate attempts were made to (i) ensure that they were from approximately the same position in the tree crown (height above ground level) and (ii) obtain samples with no or as few nodes as possible and with a diameter of 10 mm. Native branch hydraulic conductivity (K_h) was measured from branch segments of *C. tagal* in June 2012, *A. marina* in July 2012 and *R. mucronata* in January 2013. The branches were cut at least 15 cm from the target branch segment during the morning of the day of measurement. This was done under water with the help of a funnel-shaped plastic table mat

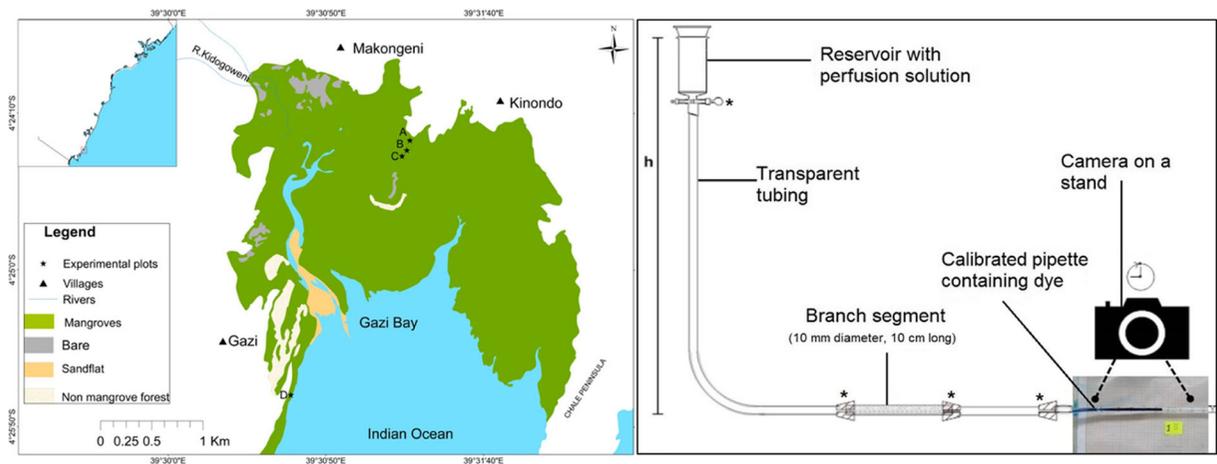


Fig. 1 **a** Map of Gazi Bay indicating the study sites where the sedimentation experiment was conducted. A: *Avicennia marina*, B: *Ceriops tagal* landward, C: *Ceriops tagal* seaward and D: *Rhizophora mucronata*. The inset shows where the study area is located within Kenya. Source: Kenya Marine and Fisheries Research Institute database. **(b)** Laboratory set-up for hydraulic

conductivity measurements. A camera is focused above a calibrated pipette laid on a graduated sheet of paper to take a series of pictures at regular intervals. h : the height of the reservoir (60–70 cm) that generates the pressure head, *: taps to start or stop flow of the perfusion solution within the tubing system. Adapted from Choat et al. (2011) and De Deurwaerder et al. (2016).

wrapped around the branch. The branches were transported to the laboratory in a bucket with the cut tips touching onto a dump rug and the foliage covered with an opaque bag to minimise transpiration.

The sampled branches were then recut under water (Hao et al. 2009) into segments of about 10 cm long. The choice of branch segment diameter (10 mm) was based on methodological bias for the branch to fit perfectly in the tubings (Fig. 1b) while the length was set after rapid assessment of vessel lengths of the three species which showed skewness towards shorter vessels. The longest vessel length was recorded in *R. mucronata* (55 cm) and the median length for the three tree species was 11.5 cm. Where appropriate length without nodes could not be obtained, the side branch was carefully cut off and the exposed surface immediately sealed with parafilm to avoid water loss. Hydraulic conductivity was measured using the set-up depicted in Fig. 1b (Choat et al. 2011). The perfusion solution used was 1.0% seawater, filtered through 0.2 μm Millipore syringe filters (Millex GS filter, Millipore Corrigtwohill Co, Cork, Ireland). This solution is similar to the ionic concentration of the sap within a mangrove stem (Scholander et al. 1966; Ball 1988; Choat et al. 2011).

The hydraulic pressure for the water flowing through the branch segments was generated by a reservoir raised at 60 to 70 cm (Fig. 1b), producing a pressure range of 5.91 to 6.5 kPa. The flow rate through the branch segment was determined by tracking the motion of dye

through a calibrated pipette (0.01/0.1 mm) connected to the distal end of the branch segment and laid on a grid paper. This was recorded at intervals of 15 to 20 s over 5 min as images which were loaded in ImageJ (1.45 s, Wayne Rasband, National Institute of Health, USA) and distances covered by the dye measured to calculate sap flow rate. From the 15 images taken per sample making a total of 720, only 490 images were used to calculate flow rate since some were unclear or distorted ($n = 490$). Native hydraulic conductivity (K_h) was then calculated as:

$$K_h = \frac{F \times L}{\Psi} = \frac{m^3 s^{-1} m}{MPa} = [m^4 s^{-1} MPa^{-1}] \quad (1)$$

where F is the flow rate [$m^3 s^{-1}$], L is the length of the branch segment [m] and Ψ is the applied pressure [MPa]. Considering that $1 m^3 = 1000 \text{ kg}$, we express the units as $\text{kg m}^{-1} s^{-1} MPa^{-1}$.

Leaf area of all leaves (A_L) from the distal end of the branch segment were measured using a Portable laser leaf area meter (CI-202, CID Bio-science, Washington, USA). The average leaf area was then used to calculate leaf-specific hydraulic conductivity (K_L) as defined in Zotz et al. (1997):

$$K_L = K_h / A_L [\text{kg m}^{-1} s^{-1} MPa^{-1}] \quad (2)$$

where A_L is the total leaf area on a given experimental branch segment.

Small discs (ca. 1 cm long) were cut from each branch segment and trimmed at their transverse section with a sledge microtome (GSL1-microtome, Zürich, Switzerland - Gärtner et al. 2014). The discs were then photographed using a camera (Olympus N547, Tokyo, Japan) attached to a stereomicroscope (Olympus SZH10, Tokyo, Japan) after which the xylem tissue proportions were measured using ImageJ (1.45 s, Wayne Rasband, National Institute of Health, USA). The mean xylem area was then used to adjust native hydraulic conductivity to obtain xylem-specific hydraulic conductivity (K_s) as defined in (Lopez-Portillo et al. 2005; Zotz et al. 1997):

$$K_s = K_h/A_X \text{ [kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}] \quad (3)$$

where A_X is the mean xylem area.

Xylem structure measurements

Two transverse sections of about 20 μm thicknesses were made from each of the branch segments used for hydraulic conductivity using a sledge microtome (GSL1-microtome, Zürich, Switzerland. Gärtner et al. 2014) after which they were stained with a safranin-alcian blue mixture. Vessel characteristics (vessel density, vessel diameters and vessel grouping) were determined in six fields of view of 0.385 mm^2 or 0.239 mm^2 in each of the two transverse sections. The fields were set within 700–1000 μm from the bark to reduce chances of including wood formed before the experimental period based on the species radial increment rates (Robert et al. 2010). Making use of the image-acquisition and archiving software CellB (Olympus Cell^B Soft Imaging System GmbH, Münster, Germany), the short and long vessel axes (a, b) were measured for 20 vessels per field of view (in total 120 per sample and 360 per treatment). All vessels in the same fields of views were then counted (20–160) and categorized according to the number of vessels per vessel group (two's three's, four's and more than four). The vessel lumen area (A_{vessel}) and potential conductive area ($A_{\text{conductive}}$) were calculated using Eqs. 4 and 5 respectively.

$$A_{\text{vessel}} = \pi \left(\frac{a}{2} \cdot \frac{b}{2} \right) \quad (4)$$

$$A_{\text{conductive}} = A_{\text{vessel}} \times \text{vessel density} \quad (5)$$

where a and b are the short and long vessel axes.

Equivalent vessel diameter (D_e , Eq. 6; Lewis 1992) was calculated to enable comparison of vessels with diverse cross-sectional shapes.

$$D_e = \sqrt{\frac{2a^2 b^2}{a^2 + b^2}} \quad (6)$$

The degree of vessel grouping was quantified based on vessel grouping index as described by Carlquist (2001), i.e. the total number of vessels divided by total number of vessel groups.

Stomata measurements

The third pair of leaves (counted from the shoot tip) was collected from all branches used for the determination of hydraulic conductivity. Stomatal imprints of 1–2 cm^2 in size were made mid length and close to the mid rib from the abaxial surface of each leaf of *C. tagal* and *R. mucronata* (Gitz and Baker 2009). For *A. marina* leaves, macerations were prepared according to Yeung (1998), using 1–2 cm^2 pieces of leaves cut from the same position as the other species. All the stomata were counted and lengths and widths of guard cells of 15 closed stomata were measured in three different fields of view (0.4 mm^2) using the image-acquisition and archiving software CellB (Olympus Cell^B Soft Imaging System GmbH, Münster, Germany), via an Olympus UC30 camera fitted on an Olympus BX60 microscope (Wisconsin-Madison, USA). Total stomatal area was calculated by multiplying stomata density (count per unit leaf area) by median stomatal area.

Statistical analysis

Data analysis was performed in STATISTICA 7.0 (StatSoft Inc., Tulsa, USA) applying a significance level of 0.05. Effect of difference in species and sedimentation level on soil redox potential was tested as a Nested mixed model using the Univariate test for significance. This was followed by a focussed test of interaction using one way ANOVA to assess differences across treatments within each of the species. This is due to the significant interaction registered among treatment, species and sampling time. Difference in response of the three tree species to sedimentation was tested using the non-parametric Kruskal-Wallis ANOVA by ranks since assumptions for parametric testing were not met even after transformation of conductivity, xylem structure and stomata properties data. The landward and seaward plots of *C. tagal* were

treated separately except for potential conductive area and total stomatal area where there was no significant difference between the two. Where differences were significant a pairwise comparison of the four treatments was done using multiple comparisons of mean ranks. In order to establish the influence of vessel grouping index on hydraulic conductivity, Spearman's Rank correlation was used to test for possible relationship.

Results

All the *A. marina* and *R. mucronata* trees survived partial burial while some level of mortality was observed in the 45 cm burial treatment of *C. tagal* where 5 out of the 17 trees died within the first six months of exposure.

Environmental variables

Redox potential values ranged between -4 to 305 mV in the *A. marina* plots and between -44 and 20 mV in the *C. tagal* and *R. mucronata* plots (Fig. 2). A univariate test of significance showed significant influence of sedimentation level, species and sampling time on soil redox potential (Table 1). The significant difference across treatments was however only confirmed in *C. tagal* and *R. mucronata* but not for *A. marina* (Table 2). Further, Fig. 2 shows that the soil redox potential values were relatively more negative in the plots of higher sedimentation treatments particularly for *C. tagal* and *R. mucronata*.

There was no systematic trend recorded in salinity ranges with sedimentation for *A. marina* and *C. tagal*. In *R. mucronata*, the salinity range (difference between maximum and minimum) varied in the order 14‰, 17‰, 22‰, and 37‰ with each successive sedimentation level

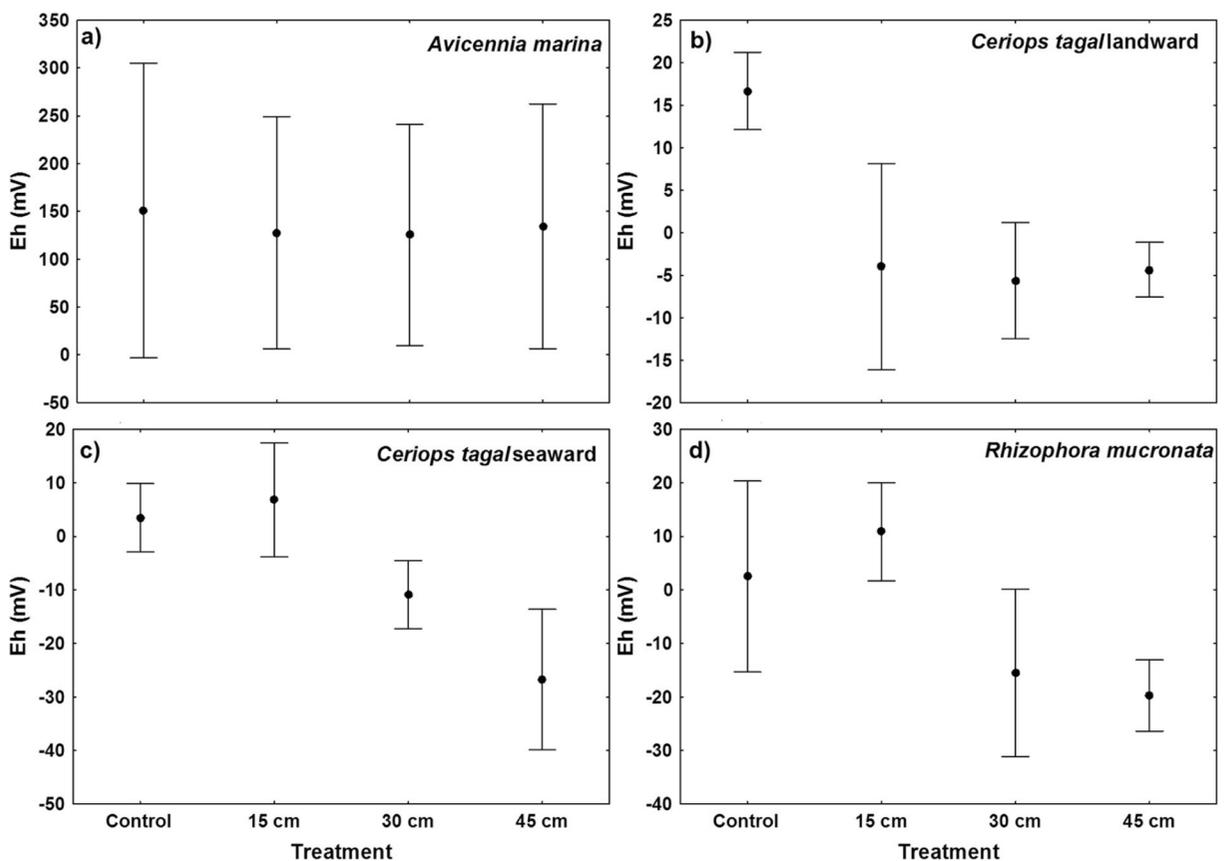


Fig. 2 Soil redox potential (Eh in mV) measured at different sediment depths (5 cm then after every 10 cm including 10 cm below original sediment level) in (a) *Avicennia marina*, (b) *Ceriops tagal* from landward plots, (c) *Ceriops tagal* from

seaward plots and (d) *Rhizophora mucronata*. Plots: marker (mean), whisker (\pm SD). Measurements were done 3 months and 6 months after partial burial

Table 1 Univariate tests of significance for soil redox potential

Effect	Degr. of - Freedom	Mean square	F	p value
Intercept	1	109,480.7	186.65	<0.001
Treatment	3	3502.2	5.97	<0.01
Species	3	142,383	242.74	<0.001
sampling time	1	97,356	165.97	<0.001
Depth	3	842.7	1.44	>0.05
Treatment*species	9	594.1	1.01	>0.05
Treatment by sampling time	3	130.3	0.22	>0.05
Species by depth	9	622	1.06	>0.05
Treatment* by species by sampling time	12	24,232.3	41.31	0.001
Depth(sampling time)	3	397.7	0.68	0.568
sampling time(Species)	0			
Species(Treatment)	0			
Error	70	586.6		

(Supplementary Table 2). This was also linked to the progressive increase in height above datum with sedimentation from control: – 3.09 m; 15 cm: – 3.31 m; 30 cm: – 3.34 m and 45 cm: – 3.52 m. The minimum salinity recorded in the 15 and 30 cm sedimentation treatments (*C. tagal*) were much lower as compared to salinity values in the control plot. Sediment nutrient analysis revealed higher phosphate, nitrate and ammonia levels in the terrestrial sediment as compared to sediment from the controls (Supplementary Table 2).

Hydraulic conductivity

Except for *C. tagal* in the seaward plots, increased hydraulic conductivity (K_L and K_S) was observed in the 15 and 30 cm sediment burial while at 45 cm, it was comparable to the controls (*A. marina* and *C. tagal*; Fig. 3a, b, c and d) or slightly higher (*R. mucronata*; Fig. 3g and h). *A. marina* showed the highest hydraulic conductivity in the 15 cm burial level (Fig. 3a and b) with both 15 and 30 cm treatments having significantly higher K_L ($H = 36.74$, $p < 0.001$, Fig. 3a) and K_S ($H = 26.69$, $p < 0.001$; Fig. 3b) compared to the controls.

C. tagal landward treatments showed different hydraulic conductivity trends from the seaward treatments, which are exposed to longer inundation periods and higher tidal flooding levels. In the branches from the landward plots, K_L was significantly higher in the 15 and 30 cm sediment burial levels as compared to the rest of the treatments ($H = 52.78$, $p < 0.001$). Branches from the highest sedimentation level (45 cm) showed similar K_L as the controls (Fig. 3c). K_S followed a similar pattern with a significantly

higher conductivity in the 15 cm level than the control (Fig. 3d). Seaward plots showed the highest conductivity in 45 cm burial level (Fig. 3e and f). K_L was significantly higher in the 30 cm burial treatment as compared to the rest of the treatments ($H = 54.75$, $p < 0.01$; Fig. 3e). Branches from trees in the 30 and 45 cm burial treatments had significantly higher K_S than the controls and those from the 15 cm burial level ($H = 43.16$, $p < 0.001$).

Hydraulic conductivity in *R. mucronata* was highest in the minimum burial treatment (Fig. 3g and h). Both K_L and K_S were significantly higher in branches from the partially buried trees compared to the controls (K_L : $H = 60.51$, $p < 0.001$, Fig. 3g; K_S : $H = 52.49$, $p < 0.001$, Fig. 3h).

Wood anatomy and stomatal area

Branches of *A. marina* from the 45 cm burial treatment showed a combination of relatively higher De (Table 3) and higher potential conductive area compared to the control (Table 4). However, these two features did not produce an increase in hydraulic conductivity at this level. The species showed the highest vessel grouping index in the moderately buried trees (15 cm) and the lowest at highest burial (45 cm) (Table 3). This trend of vessel grouping index with burial was similar to the observed hydraulic conductivity (Fig. 3a and b). The total stomatal area in *A. marina* showed no distinct trend with increasing sediment burial (Table 4).

Partially buried *C. tagal* trees from landward plots had branches with narrower vessels (Table 3) as compared to the controls, dipping significantly at the 30 cm burial level ($H = 155.88$, $p < 0.001$). These trees (30 cm burial level), also showed the highest vessel grouping

Table 2 One way ANOVA results on difference across treatments in the 3 mangrove tree species studied

Effect = soil redox potential	df	F	Mean square	p value
Among species	3	44.72	142,270.60	<0.00001
Treatment in <i>A. marina</i>	3 (26)	0.05	867.80	>0.05
Treatment in <i>C. tagal</i> Landward	3 (25)	13.15	727.57	<0.0001
Treatment in <i>C. tagal</i> Seaward	3 (24)	17.64	1661.42	<0.00001
Treatment in <i>R. mucronata</i>	3 (26)	10.18	1648.71	<0.001

index (Table 3). The branches from seaward plots showed different trends with a combination of significantly wider vessels and lower vessel grouping in the branches from partially buried trees as compared to the controls (Table 3). Vessel diameters were positively correlated with Ks ($R = 0.55$, $p < 0.05$) while vessel grouping index did not correlate with the hydraulic conductivity rates observed. Response in potential conductive area and stomatal properties were similar in the two locations as both landward and seaward trees showed lower values in the partially buried trees as compared to the controls (Table 3).

In *R. mucronata*, De was significantly higher than the controls in the highest level of partial burial (45 cm, Table 3). The vessel grouping index increased with the level of sediment burial ($H = 134.8$, $p < 0.001$), reaching a maximum in the 30 cm burial treatment (Table 3). Although the vessel grouping pattern did not match the trend of the observed hydraulic conductivity (Fig. 3g and h; Table 3), Spearman's Rank-Order correlation revealed a positive correlation between vessel grouping index and Ks irrespective of sedimentation level ($R = 0.61$, $p < 0.05$). A multiple comparison of means showed that *R. mucronata* had significantly higher potential conductive area with 15 and 30 cm burial ($p < 0.01$), peaking in the 30 cm treatment (Table 4). Stomatal area was relatively higher than the control in the leaves from the 30 and 45 cm burial level (Table 4) but none of the treatments differed significantly from the controls ($H = 4.02$, $p > 0.05$).

Discussion

Increased sedimentation may increase hydraulic conductivity

After 14 months of experimental burial, a higher hydraulic conductivity was observed for the 15 and 30 cm

sedimentation treatments in all three mangrove species and there was no significant reduction in hydraulic conductivity with respect to the control in the 45 cm burial treatment in any of the species (Fig. 3). The results support hypothesis on increased hypoxia as a result of sedimentation and development of adaptive features following burial at least in some species. From these results, three possible scenarios can be derived that could have resulted in the observed hydraulic conductivity pattern:

(1) *Changes in environmental parameters in response to sedimentation*

In line with our hypothesis, the results showed significant increase in hypoxia (more negative soil redox potential) as a result of sedimentation treatment at least for *C. tagal* and *R. mucronata* (Tables 1 and 2, Fig. 2). However, the redox potential values in the treatments remained within the ranges associated with higher inundation classes in mangroves (Matthijs et al. 1999). As a result, reduction of hydraulic conductivity associated with hypoxia (Laur and Hacke 2014) was not observed. The increase in hydraulic conductivity with intermediate levels of burial can be attributed to the higher nutrient levels measured in the terrestrial sediment added as compared to the controls (Supplementary Table 2). Studies have shown that the process of sedimentation in itself is associated with nutrient input (Alongi et al. 2005; Lovelock et al. 2010) and that nutrient -enrichment of mangrove in turn may result in up to 6 -fold increase in hydraulic conductivity (Lovelock et al. 2004).

(2) *Changes in anatomical traits associated with sedimentation*

Alterations in xylem structure (vessel grouping and vessel sizes) were observed after 14 months of partial burial (Table 3; Table 4) hence supporting the third hypothesis of the study. Such induced adjustments in xylem

Table 3 Equivalent vessel diameter (De) and vessel grouping index (VGI) in the three studied species (*Avicennia marina*, *Ceriops tagal*, and *Rhizophora mucronata*) after 14 months of

exposure to experimental sediment burial simulating three levels of sedimentation (15, 30 and 45 cm). (Kruskal-Wallis and multiple comparisons of mean ranks)

Species	Treatment	Equivalent vessel diameter (De)			Vessel grouping index (VGI)		
		Median	Lower Q	Upper Q	Median	Lower Q	Upper Q
<i>A. marina</i>	Control	37.54	24.15	46.32	1.79	1.60	1.93
	15 cm	36.47	25.10	48.24	2.11	1.99	2.15
	30 cm	38.94	27.20	49.00	1.96	1.70	2.03
	45 cm	39.78	29.94	50.64	1.63	1.55	1.65
<i>C. tagal</i> Landward	Control	31.81	27.67	34.84	1.19	1.16	1.28
	15 cm	30.49	27.27	32.90	1.12	1.08	1.21
	30 cm	25.39	21.54	28.48	1.29	1.25	1.42
	45 cm	29.64	25.84	33.17	1.18	1.13	1.22
<i>C. tagal</i> Seaward	Control	28.09	23.51	31.80	1.30	1.20	1.31
	15 cm	31.84	27.77	34.72	1.13	1.10	1.16
	30 cm	31.83	26.98	35.42	1.08	1.06	1.11
	45 cm	33.89	29.98	36.95	1.19	1.13	1.26
<i>R. mucronata</i>	Control	42.01	37.27	44.05	1.21	1.17	1.26
	15 cm	43.09	37.48	47.31	1.25	1.23	1.26
	30 cm	38.79	33.84	45.07	1.58	1.52	1.60
	45 cm	48.59	41.99	52.98	1.33	1.31	1.34

The bold values are significantly different from the controls

structure have also been observed following metal contamination and imposed drought in red maple where reduction in Ks was also noted (de Silva et al. 2012). In our study, both vessel grouping and diameter were found to be sensitive to sedimentation in differing magnitude and directions among the species studied. However, only vessel sizes in *C. tagal* and potential conductive area in *R. mucronata* appeared to directly explain the observed variations in hydraulic conductivity.

Considering the Hagen-Poiseuille's law, wider vessels are more efficient in sapflow than those with smaller diameters (Tomlinson 1994; Choat et al. 2007). Additionally, high potential conductive area could provide more alternative routes for xylem sap to circumvent air-filled vessels and vessel parts (Cruziat et al. 2002). A combination of increased conductive area and high vessel grouping index, which also enhances hydraulic safety (Awad et al. 2010; Choat et al. 2011), could have resulted in increased hydraulic conductivity for the 15 cm burial level, in which branches had a combination of the two features as in *R. mucronata* (Table 3).

Reduced stomatal area was observed in response to partial burial in *C. tagal* (Table 3). Reduction in total stomata area could be interpreted as an attempt to lower

transpiration rates against decreased water uptake imposed by large sedimentation (Tomlinson 1994) thus preventing critically negative xylem pressure. This is in line with findings by Lake et al. (2001) showing that plants can adjust their stomata development in newly formed leaves in response to prevailing conditions. This enables them to regulate transpiration thus ensuring that sap flow is maintained (Meinzer and Grantz 1990). There was however large variations observed in stomatal area of leaves produced by *A. marina* and *R. mucronata* which might have hindered detection differences statistically. In addition, hypoxia which is otherwise known to be associated with stomatal area in various plants including mangrove tree species (Sojka 1992) remained within normal ranges of a tidal flat (Matthijs et al. 1999; Dahdouh-Guebas et al. 2004).

(3) Other features not measured in the current study

Sedimentation may have a similar effect as drought by reducing water uptake by the roots (Tomlinson 1994; Sperry et al. 1998), as such one would expect affected trees to acclimatise through reduction in Ks and K_L

Table 4 Vessel lumen area per unit xylem area (potential conductive area) and total stomatal area per unit leaf area in the three studied mangrove tree species (*Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*) exposed to partial sediment burial

simulating three levels of sedimentation (15, 30 and 45 cm) for 14 months. N/s: not significantly different from the control ($p > 0.05$); **C. tagal* from landward and seaward were not significantly different from each other. Q is quartile

Species	Treatment	Vessel lumen area ($\mu\text{m}^2/\text{mm}^2$) $\times 10^4$				Total stomata area ($\mu\text{m}^2/\text{mm}^2$) $\times 10^4$			
		Median	Lower Q	Upper Q	<i>p</i> value	Median	Lower Q	Upper Q	<i>p</i> value
A. marina	Control	6.59	6.30	7.10	N/s	3.55	2.93	3.87	
	15 cm	7.96	6.40	8.51		3.02	2.83	3.26	
	30 cm	7.21	5.14	9.10		4.51	4.15	4.94	N/s
	45 cm	8.45	6.43	11.14		3.18	2.36	4.14	
*C. tagal	Control	7.08	5.38	7.56	N/s	6.03	5.04	6.46	
	15 cm	7.31	6.79	7.78		4.08	3.69	4.91	N/s
	30 cm	5.73	5.04	6.34		3.71	3.41	4.02	<0.01
	45 cm	6.79	4.80	7.89		4.74	3.67	5.46	N/s
R. mucronata	Control	4.76	3.60	5.73		8.75	8.15	9.28	
	15 cm	8.4	6.96	9.95	<0.01	8.77	8.48	8.94	
	30 cm	10.14	8.25	10.85	<0.001	9.51	8.48	9.99	N/s
	45 cm	5.62	4.99	7.54	N/s	9.45	8.49	10.38	

The bold values are significantly different from the controls

mainly as a means to preserve the little available water (Ladjal et al. 2005) or reduction through induction and spread of embolism in otherwise functional vessels (Lens et al. 2013). The observed increase in hydraulic conductivity suggests involvement of ion-mediated increase in K_s as has been elaborated by Hacke (2014) with possible embolism related to sedimentation. The bell shaped curve however indicates that further sedimentation (larger than 45 cm) could have a negative effect on hydraulic conductivity. Further, the consistent K_L pattern in all the species also suggest an overriding influence of increased leaf area on hydraulic conductivity upon sediment burial.

Interspecific variations in response to sedimentation

The interspecific variations in hydraulic conductivity values (K_L and K_s) observed among the trees under different treatments can be attributed to anatomical variations among mangrove species including intervessel pit characteristics (Choat et al. 2007; Schmitz et al. 2008). Consequently, different mangrove tree species will have varying levels of resilience capacity and thresholds to large sedimentation events with possible death occurring above such thresholds due to hydraulic failure (McDowell et al. 2013; Rowland et al. 2015). However, the death of a few *C. tagal* trees observed for this experiment could not be attributed to hydraulic failure.

The results suggest species-specific adaptive strategies in partially buried mangrove trees. In *A. marina* wood which is characterised by narrow vessels (Robert et al. 2009a), the branches developed higher vessel grouping as a result of burial. While vessel grouping is associated with hydraulic safety (Carlquist 1984, 2009; Scholz et al. 2013), others have been of the view that extensive vessel connectivity increase probability of spread of embolism (Loepfe et al. 2007; Martínez-Vilalta et al. 2012). In which case, the argument by Lens et al. (2011) that grouping is compensated for by vessel diameter under water limiting conditions is thus upheld in this study. In *R. mucronata*, there was a significant increase in vessel grouping in the 30 and 45 cm buried trees signifying a change to more xeric conditions (Carlquist 1984). Taking into account the relatively high tolerance levels of *Rhizophora* species to hypoxia (Twilley et al. 1996) associated with sedimentation in this study, individual differences in vessel grouping index could also be associated to available packing space for the vessels to occupy in the xylem (Martínez-Vilalta et al. 2012).

Within species variations in response to sedimentation

There was a disparate response between landward and seaward *C. tagal* plots. In the landward plots there was a threshold above which conductivity decreased and

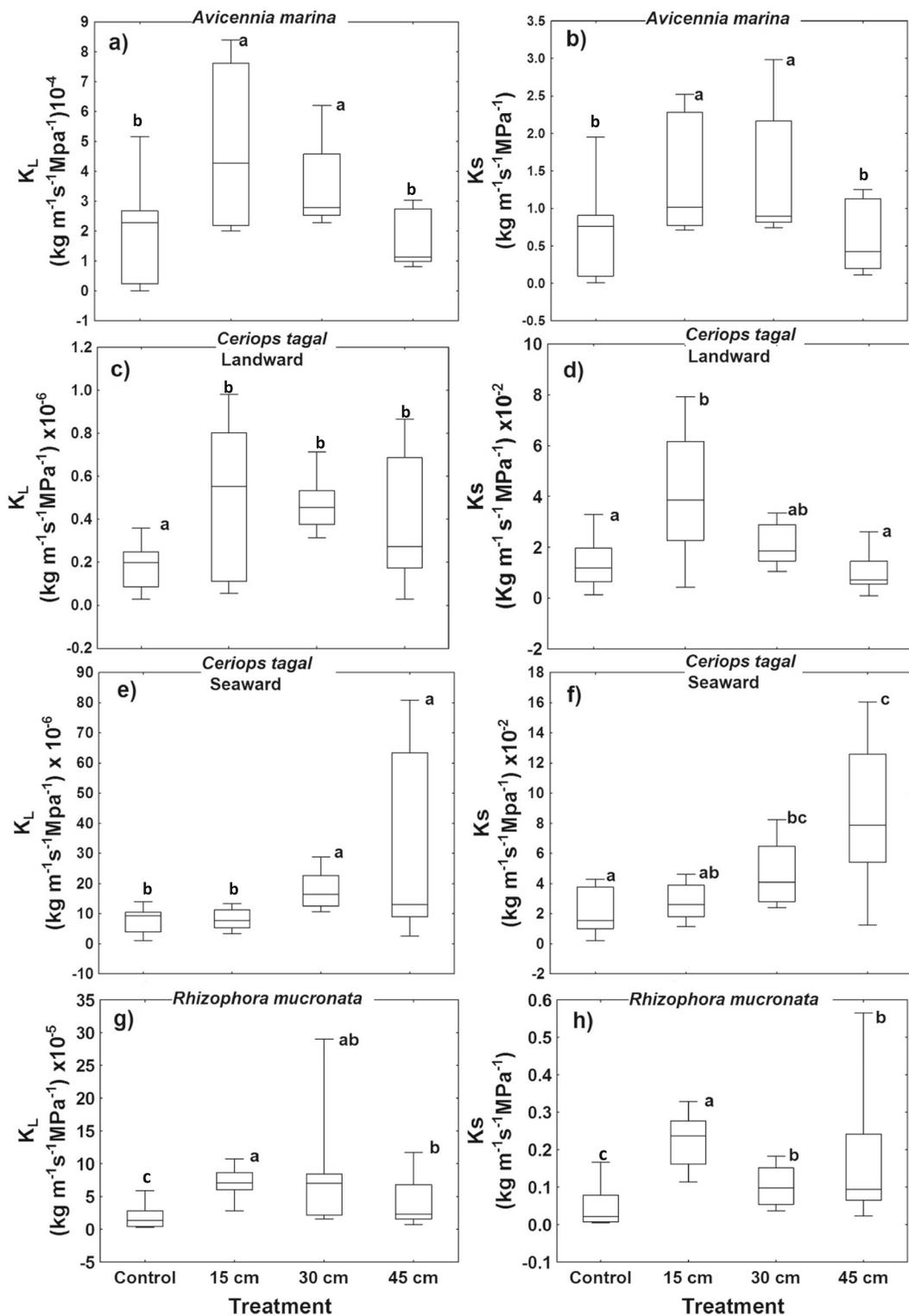


Fig. 3 Branch hydraulic conductivity, standardized for total branch leaf area (K_L ; a, c, e & g) and for xylem area (K_S ; b,d,f & h) of the three studied species (*Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata*) after 14 months of experimental

sediment burial simulating three sedimentation levels (15, 30 and 45 cm). Letters indicate significant differences. Box plots: line (median), box (25–75%), whiskers (maximum and minimum values)

became comparable to the control trees (Fig. 3c and d), the seaward plots had increased conductivity (corrected for xylem area, K_s) reaching a maximum (two-fold of the control) at the highest sedimentation level (Fig. 3f). This was coupled with local differences in anatomical responses as the trees may show: (i) lower vessel grouping index but an increase in vessel diameter and potential conductive area, or (ii) higher vessel grouping with reduced vessel diameter, or (iii) a reduction in both vessel grouping and potential conductive area but increasing vessel diameter depending on the intertidal position.

Such variations can be associated with local differences in salinity fluctuations, nutrient availability or inundation durations within an intertidal area (Lovell et al. 2006; Schmitz et al. 2006, 2007; Robert et al. 2009b). Salinity gradients and varying inundation frequencies across the tidal flat, for instance has been found to result in production of variant vessel characteristics (density and sizes) in *A. marina* and *R. mucronata* (Schmitz et al. 2006; Robert et al. 2009a.), which in turn influence hydraulic conductivity (Curtis and Ackerly 2008).

Resilience of mangrove tree species to large sedimentation events

The results of this study showed adaptation mechanisms that are mostly species- and location specific and consist of: (i) modification of hydraulic architecture allowing to avoid or overcome cavitation and its effects; or (ii) reduction in stomatal area which minimises transpiration for an optimal water transport capacity. Considering the relatively short period (14 months) within which the anatomical changes were observed, the high plastic growth nature of plants (Jain and Minocha 2000) is emphasised. This is an indication of resilience of mangrove forests to changes associated with sedimentation. However, mangroves are not solely affected by sedimentation but face a variety of impacts; we may thus not yet extrapolate the current results to incidence of partial burial that mangroves can withstand in general.

Conclusions

Following 14 months of experimental partial burial simulating three levels of large sedimentation events, the results show that mangrove trees may acclimatise to large and sometimes episodic sedimentation events at

least under the conditions that our experiment was set. The results further suggest rapid (within 14 months) adaptation ability to sedimentation-induced stress, which we equate to physiological drought. As stated in our hypothesis, vessel grouping, diameter and potential conductive area are all sensitive to sedimentation but to varying degrees among species and even individuals of the same species in the same geographic location. It is however, not always the case that the anatomical changes are reflected in hydraulic conductivity.

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