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The bark and wood properties of *Bruguiera gymnorrhiza* and *Rhizophora stylosa* trees in riverine mangrove forest

Trevor G. Jones[1] and Shin Watanabe[2]

[1] *The New Zealand Institute for Plant and Food Research Limited, Private Bag 11600, Palmerston North 4442, New Zealand*
[2] *Iriomote Station, Tropical Biosphere Research Center, University of the Ryukyus, 870 Uehara, Taketomi, Yaeyama, Okinawa, 907-1541, Japan*

*Corresponding author: trevor.jones@plantandfood.co.nz

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Abstract

Background: The mangrove species *Bruguiera gymnorrhiza* (L.) Lam. and *Rhizophora stylosa* Griff. are found in riverine mangrove forest, where the trees occur in mixed forest. They have different ecological traits and supporting buttress root systems. However, little is known about the bark and wood structural properties of the trees which are important when using biomechanical approaches to understand the ecological differences between species. Here we test the hypothesis that the structural properties of the trees are influenced by the ecology of these species in riverine mangrove forest.

Methods: Plots were established in mixed forest of *B. gymnorrhiza* and *R. stylosa* in riverine mangrove forest on Iriomote Island in Okinawa, Japan. Selected trees from the two species were sampled to evaluate the bark and wood properties of the stems, branches and roots. The data were analysed and compared for the two mangrove species.

Results: *Bruguiera gymnorrhiza* and *R. stylosa* have differences in their bark and wood properties. *R. stylosa* trees have thicker bark and higher bark density, and wood of higher density, strength, stiffness, and hardness. This applies to the stems and roots of *R. stylosa* trees, and supports the compressive buttresses, and exposed tidal positions of this light demanding pioneer species. *Bruguiera gymnorrhiza* trees have a higher proportion of wood in the stems and branches, and less in the roots, which can be attributed to the risk of canopy damage, and the presence of tensile buttresses, in this shade-tolerant gap-phase species.

Conclusions: Differences in the bark and wood properties of the stems, branches and roots, were consistent with the ecological traits of *B. gymnorrhiza* and *R. stylosa*, and the structural properties of the buttress root systems. The knowledge will aid understanding of the distribution of these species in riverine mangrove forest.

Keywords: *Bruguiera gymnorrhiza*, *Rhizophora stylosa*, trees, bark, wood properties

Introduction

The riverine mangrove forests on Iriomote Island in Okinawa, Japan, are dominated by the mangrove species *Bruguiera gymnorrhiza* (L.) Lam. and *Rhizophora stylosa* Griff. (Kikuchi et al. 1978; Nakasuga et al. 1982; Enoki et al. 2009). *Rhizophora stylosa* is found in the lower reaches of the rivers, where the stem diameters and growth rates of the trees are greater close to the riverside, while *B. gymnorrhiza* is found throughout the tidal range of the rivers, but the stem diameters of the trees are greater further from the river mouth and riverside (Enoki et al. 2009).

These two mangrove species differ in their ecological traits, with *R. stylosa* being a light demanding pioneer species, while *B. gymnorrhiza* is a shade-tolerant gap-phase species (Kitao et al. 2003). Saplings of *B. gymnorrhiza* have been observed to grow in canopy gaps created by a single tree, where *R. stylosa* does not grow (Enoki et al. 2009). Seedlings of *R. stylosa* have a greater tolerance of tidal flooding (He et al. 2007) and develop a spreading root system of aerial prop roots (Figure 1), that function as compressive buttresses. *B. gymnorrhiza* trees develop stilt roots close to the stem (Figure 1, Tomlinson 1986) that function as tensile

FIGURE 1: The buttress root systems of mangrove trees. Left: the stilt roots of a *Bruguiera gymnorrhiza* tree. Right: the aerial prop roots of *Rhizophora stylosa* trees.

buttresses, and are less stable in exposed situations (Vogel 1996).

The compressive buttressing of *R. stylosa* involves the development of a stiff, wide base, that acts primarily as a set of compression-loaded buttresses on the downwind side of the trees (Vogel 1996). This arrangement increases the weight of the roots and soil, and the force that must be applied to uproot the trees, by moving the pivot or hinge point of the root system further from the base of the tree (Nicoll & Ray 1996). The effectiveness of compressive buttressing is improved if the stems of the trees have high stiffness, by minimizing the downwind drift of the centre of gravity in the wind (Vogel 1996).

The tensile buttressing of *B. gymnorrhiza* involves the development of tall, narrow, plank-like buttresses close to the stem, that are primarily loaded in tension on the upwind side of the trees (Vogel 1996). The height and narrow width of these buttresses limit in their ability to withstand compressive loads without buckling. Stabilizing the centre of gravity in the wind with a very stiff stem, should be less important than in compressive buttressing (Vogel 1996).

Studies where data have been collected to develop allometric equations for predicting the biomass of these mangrove species have yielded information on wood density. These observations of the tree stem density of these mangrove species are consistent with the differences in their root systems. Stems of *R. stylosa* and *B. gymnorrhiza* trees growing in Queensland, Australia, had a mean combined wood and bark density of 810 and 665 kg m^{-3}, respectively (Clough & Scott 1989), and the stems of *B. gymnorrhiza* trees growing in Indonesia and Thailand had a mean wood density of 699 kg m^{-3} (Komiyama et al. 2005). However, more detailed information is needed on the structural properties of the tree stems, branches and roots of these species, to underpin biomechanical investigations into the functioning of these different buttress root systems, and the ecology of these two species in riverine mangrove forest.

In this study, we tested the hypothesis that the structural properties of the trees are influenced by the ecology of the two species in riverine mangrove forest. This was investigated by evaluating the variation in the bark and wood properties of the stems, branches and roots of *R. stylosa* and *B. gymnorrhiza* trees in riverine mangrove forest in Funaura Bay on Iriomote Island, Japan. Plots were established in a mixed riverine mangrove forest of the two species, and trees were sampled to assess the longitudinal patterns of variation in the bark and wood properties of the tree stems, branches and roots. Differences between the two mangrove species were compared and discussed in terms of the ecological traits and buttress root systems of the species.

Methods

Study area

The study area of Funaura Bay on Iriomote Island in Okinawa, Japan (Figure 2) has a humid subtropical climate with a mean annual temperature of 23.5 °C, and mean annual rainfall of 2321 mm year^{-1} (during the period 1979-2009), at a weather station in the area (24°23’N, 123°45’E). The riverine mangrove forest in Funaura Bay comprises medium to tall, closed-canopy

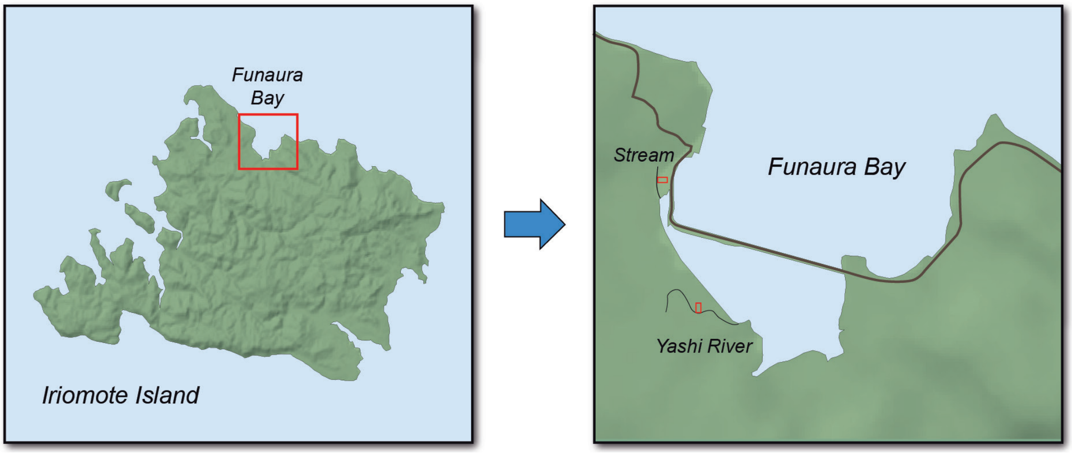


FIGURE 2: The location of Funaura Bay on Iriomote Island in Okinawa, Japan, and the mangrove forest plots (red rectangles) on the Yashi River and a stream flowing into Funaura Bay. Maps by Geographx Ltd.

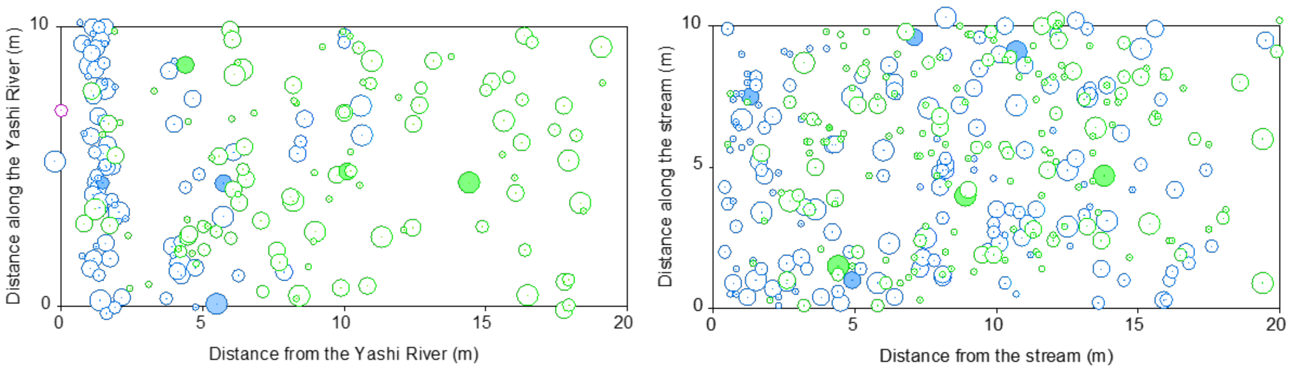
mixed forest of *Rhizophora stylosa* and *Bruguiera gymnorrhiza*, with trees of *Avicennia marina* (Forssk.) Vierh., and *Kandelia obovata* Sheue, Liu and Yong, along the river's edge.

Forest plots

Two plots were established in the riverine mangrove forest along the Yashi River and a stream that flows into Funaura Bay, in 2009 and 2010 (Figure 2). Rectangular plots (10 × 20 m) were orientated adjacent to the river and stream bank and extended 20 m perpendicular to the river and stream. The plots were characterised by a topographic gradient of increasing elevation with distance from the river and stream. The spatial location of all the trees in the plots was mapped (Figure 3), using a Vertex IV ultrasound instrument (Haglöf Sweden) and the triangulation method of Quigley and Slater (1994). Species information was record for each tree, and the canopy position of all live trees was classified as either: dominant, co-dominant, intermediate, overtopped (as defined by Cole et al. 1999). Trees greater than 1.3 m tall had their diameter at breast height (DBH at 1.3 m) and height to the first live branch and top of the tree crown measured. Heights were measured as the linear vertical height from the ground to the branch, or top of the tree crown.

Tree sampling

Seven trees each of *B. gymnorrhiza* and *R. stylosa* were sampled from the two plots, comprising three trees of each species from the Yashi River plot, and four trees of each species from the stream plot (Figure 3). The trees were single-stemmed and were selected based on the cumulative biomass distribution for each species. Tree biomass was assumed to be proportional to DBH^k, a relationship that has been found to apply to mangrove



R. stylosa trees: Dominant; Co-dominant; Intermediate; Overtopped;

B. gymnorrhiza trees: Dominant; Co-dominant; Intermediate; Overtopped

Kandelia obovata tree: Intermediate

FIGURE 3: The locations of the mangrove trees in the plots along the Yashi River (left) and the stream (right) in Funaura Bay. The size of the circles indicates the crown position of the trees, and the filled circles are the trees sampled for bark and wood properties.

species, where k is between 2 and 3 (Clough & Scott 1989). Using a value of k = 2.5, one tree of each species was sampled at the 10th percentile of the cumulative biomass distribution from the stream plot, and at the 25th, 50th and 75th percentiles of the cumulative biomass distributions from the stream and Yashi River plots. Trees of the two species were sampled in the plots to cover an overlapping range of distance from the stream and Yashi River. This ensured the sampled trees were representative of the biomass distributions, and comparable between the two species.

Sampled trees were felled at 0.3 to 0.5 m height above the ground. Stem discs were cut from all the trees, at 1 m height intervals along the stems, and at breast height (1.3 m). Branch discs were cut from the stream plot trees. One live branch was sampled in each 1 m height interval from the base of the green crown, and branch discs were cut at 20 cm intervals along the main stem of the branches. Above- and below-ground roots were sampled from the stream plot trees, and root discs were cut at 20 cm intervals along the first order roots, and the branched second and third order roots.

Disc diameter, wood density, acoustic velocity, dynamic MOE, and eccentricity

Diameters of the stem, branch and root discs, over and under the bark, were measured using a diameter tape or callipers. The slenderness of the tree stems and branches were calculated from the measurements of the stem length and diameter at breast height inside bark, and branch length and branch basal diameter inside bark, using the following equation:

$$\textit{Slenderness} = \textit{length}/\textit{diameter} \tag{1}$$

Green volume of the bark and wood of the discs was measured by the water displacement method and their oven-dry weight was measured after drying at 103 °C to constant weight. Basic density of the wood and bark was calculated from these measurements, using the following equation:

$$\textit{Basic density} = \textit{oven-dry weight}/\textit{green volume} \tag{2}$$

The average (volume-weighted) basic densities of the bark and wood of the stems, branches and roots were calculated from the disc measurements.

Acoustic velocity of the wood was measured on sections of the stem, branch and root discs, collected adjacent to those locations where the wood density discs were collected from the felled trees. Discs were air-dried and the transverse surfaces were prepared using a disc-surfacing saw (Lee & Brownlie 2009). Two ultrasonic transducers (500 MHz) were placed at opposing points on the disc transverse surfaces using pneumatic rams, and the time-of-flight for the acoustic wave to travel between them was measured (Emms & Hosking 2006). The distance between the two ultrasonic transducers was measured using digital callipers, and the acoustic velocity was calculated using the following equation:

$$\textit{Acoustic velocity} = \textit{distance between transducers}/\textit{time of flight} \tag{3}$$

Acoustic velocity was measured longitudinally, at 10 mm intervals from pith-to-bark, on four equidistant radii on each disc. The average (area-weighted) disc acoustic velocity was calculated from these measurements. From these measurements of acoustic velocity of the stem, branch and root discs, and wood basic density of the adjacent discs, the ultrasonic-measured dynamic modulus of elasticity (MOE) of the wood was calculated using the following equation:

$$\text{Dynamic MOE} = \rho V^2 \tag{4}$$

where ρ is the wood basic density, and V is the wood acoustic velocity. The average (volume-weighted) wood dynamic MOE of the stems, branches and roots were calculated from the disc measurements.

The eccentricity of the wood was measured on the root discs. The major and minor radii of the wood were measured at right angles on each air-dried disc, and the eccentricity was calculated using the equation:

$$\textit{Eccentricity} = \sqrt{1} - (b^2/a^2) \tag{5}$$

where a and b are the major and minor radii, respectively.

Small clears preparation

Small clear specimens of wood were cut for strength and hardness testing, from short billets taken at breast height (1.3 m) from four trees of each species. Up to four pith-to-bark strips were cut from each billet, depending on the billet diameter. One small clear was cut from each strip, adjacent to the bark, with dimensions 20 × 20 × 300 mm (tangential, radial, longitudinal directions) for static bending tests, and 20 × 20 × 60 mm (tangential, radial, longitudinal directions) for compression strength tests. The small clear specimens from the static bending tests, and additional specimens cut from the ends of the compression strength test samples, were used for hardness testing. The small clear specimens were conditioned at 20 °C and 65% relative humidity for four weeks prior to testing.

Small clear specimen testing

The dimensions and weight of the small clear specimens were measured to determine the moisture content and wood density. These were calculated using the equations:

$$\textit{Moisture content} = (\textit{weight at test} - \textit{oven-dry weight}/\textit{oven-dry weight}) \times 100 \tag{6}$$

$$\text{Wood density} = \textit{oven-dry weight}/\textit{volume at test} \tag{7}$$

where the small clears were dried to constant weight at 103 °C following testing, and the volume at the time of testing was measured using callipers.

The static bending modulus of elasticity (MOE) and modulus of rupture (MOR) of the small clear specimens were measured in accordance with ASTM Standard D143-94 (2000), using an Instron universal testing machine and three-point static bending over a 280 mm span. Centre-point loading was applied on the radial face at a speed of 10 mm min^{-1}, until failure occurred. MOE and MOR were calculated using the equations:

$$\textit{Static bending MOE} = PL^3/4bd^3\Delta \quad (8)$$

$$\textit{Static bending MOR} = 3PL/2bd^2 \quad (9)$$

where P = load at some point below the proportional limit for *MOE*, and the maximum load for *MOR*, L = distance between the supports, b = width, d = depth, Δ = deflection corresponding to the load P.

Dynamic modulus of elasticity (MOE) was calculated from measurements of wood density and acoustic velocity (Emms & Hosking 2006) in the longitudinal direction of the 20 × 20 × 60 mm compression strength small clears, using the same method as for the wood discs and equation 4.

Compression strength parallel to the grain of the 20 × 20 × 60 mm small clear specimens was measured in accordance with ASTM Standard D143-94 (2000), using an Instron universal testing machine and a loading speed of 0.5 mm min^{-1}.

Janka hardness of the wood on the radial and tangential faces of the small clear specimens was measured in accordance with ASTM Standard D143-94 (2000), using an Instron universal testing machine. Test values on the radial and tangential faces were averaged.

Statistical analysis

Analysis of variance (ANOVA) was used to examine the main and interactive effects of the plots and mangrove species on the properties of the *B. gymnorrhiza* and *R. stylosa* trees. Tukey's test was used to provide multiple comparisons of the plot and mangrove species tree means. Differences in the properties of the two mangrove species were compared using a t-test. The statistics were computed using the GenStat statistical software package (Version 14.2; VSN International Ltd, UK).

Results

Forest plots

The riverine mangrove forest in the Yashi River and stream plots, comprised mixed forest of *B. gymnorrhiza* and *R. stylosa* trees (Figure 3). The *R. stylosa* trees dominated the forest adjacent to the Yashi River, with the *B. gymnorrhiza* trees becoming more frequent and dominant with distance from the river. The stream plot showed a similar, but less pronounced pattern, with the *R. stylosa* trees dominant in much of the plot.

The *B. gymnorrhiza* and *R. stylosa* trees in the Yashi River plot were similar in height and stem diameter, and were larger than those in the stream plot ($P < 0.05$) (Table 1). The shorter height and smaller stem diameter of the *B. gymnorrhiza* trees in the stream plot, can be attributed to the large number of sapling trees of *B. gymnorrhiza* that were present, with the *R. stylosa* trees having a less skewed stem diameter distribution with fewer sapling trees. The difference in the forest structure, indicates that many of the trees in the stream plot, were younger than those in the Yashi River plot.

Sampled trees

Sampled trees of *B. gymnorrhiza* and *R. stylosa* from the two plots, showed no significant species differences for stem diameter and height, but the *B. gymnorrhiza* trees had a greater depth of live crown, and branches of larger basal diameter ($P \leq 0.05$) (Tables 2 and 3).

Stem properties of the trees

The stems of the *R. stylosa* trees had greater slenderness, thicker bark, and higher bark and wood density, and wood dynamic modulus of elasticity (MOE), compared with *B. gymnorrhiza* ($P < 0.05$) (Table 3, Figure 4). The species differences in bark and wood properties were observed both in small and large diameter trees, and with increasing height in the stems (Figure 4).

Comparison of the small and large diameter trees showed the bark was thicker in the stems of the large diameter trees of *B. gymnorrhiza* ($P < 0.05$), but in *R. stylosa* the difference was small and not significant ($P = 0.25$) (Figure 4). Bark density was similar in the small and large diameter trees of *R. stylosa*, while the

TABLE 1: Number and properties of the *B. gymnorrhiza* and *R. stylosa* trees in the forest plots. Mean and range of individual tree values in brackets. Different letters indicate significant differences in mean values between the plots and species ($P < 0.05$).

Tree properties	Yashi River Plot		Stream Plot	
	B. gymnorrhiza	***R. stylosa***	***B. gymnorrhiza***	***R. stylosa***
Number of trees	109	89	170	193
Diameter at breast height (cm)	6.7 (1.8-15.0) b	6.2 (2.2-12.7) b	3.5 (0.8-11.0) a	4.0 (0.6-10.5) a
Height (m)	**5.0 (1.2-7.2) d**	**3.9 (1.2-7.2) c**	**2.5 (0.8-5.5) a**	**3.2 (0.7-5.9) b**
Depth of live crown (m)	**2.6 (0.1-5.5) b**	**1.6 (0.3-3.5) a**	1.6 (0.2-5.0) a	1.5 (0.2-4.0) a

TABLE 2: Analysis of variance comparing the properties of the sampled trees in the forest plots and mangrove species. All values shown are *P*-values. Seven trees were sampled of each species in the forest plots.

Source of variation	Diameter at breast height	Height	Depth of live crown	Branch basal diameter	Stem bark thickness	Stem bark density	Stem wood density	Stem wood dynamic MOE
Plot	**0.05**	**<0.001**	0.09	**<0.001**	**0.04**	**0.05**	0.67	0.40
Species	0.13	0.37	**0.001**	**0.05**	**0.03**	**<0.001**	**<0.001**	**<0.001**
Plot × Species	0.30	0.28	0.71	0.75	0.49	**0.01**	0.92	0.65

large diameter trees of *B. gymnorrhiza* had higher bark density ($P < 0.05$). In both species, the small and large diameter trees had similar wood density and dynamic MOE.

The stem bark thickness of both species, the bark density of *B. gymnorrhiza*, and wood density of *R. stylosa*, declined with height in the tree stems (Figure 4). Bark density of *R. stylosa*, wood density of *B. gymnorrhiza*, and wood dynamic MOE of both species, increased with height in the lower stem, and then declined with height in the upper stem of the trees.

The proportion of stem bark and wood was different for the two species, with *B. gymnorrhiza* having a lower proportion of bark, and a higher proportion of wood, compared with *R. stylosa* (Figure 5). In *B. gymnorrhiza*, the proportion of bark declined slightly with height in the lower stem, and increased with height in the upper stem. In *R. stylosa*, the proportion of bark increased with height in the stems.

The small clears cut at breast height (1.3 m) from the stems of the *R. stylosa* trees, showed higher wood density, dynamic MOE, compression strength, and Janka hardness, compared with *B. gymnorrhiza* ($P < 0.05$) (Table 4). Wood static bending modulus of elasticity (MOE) and modulus of rupture (MOR) were higher for *R. stylosa*, but the differences were not significant ($P = 0.33$ and $P = 0.07$, respectively) due to the smaller number of samples for these measurements.

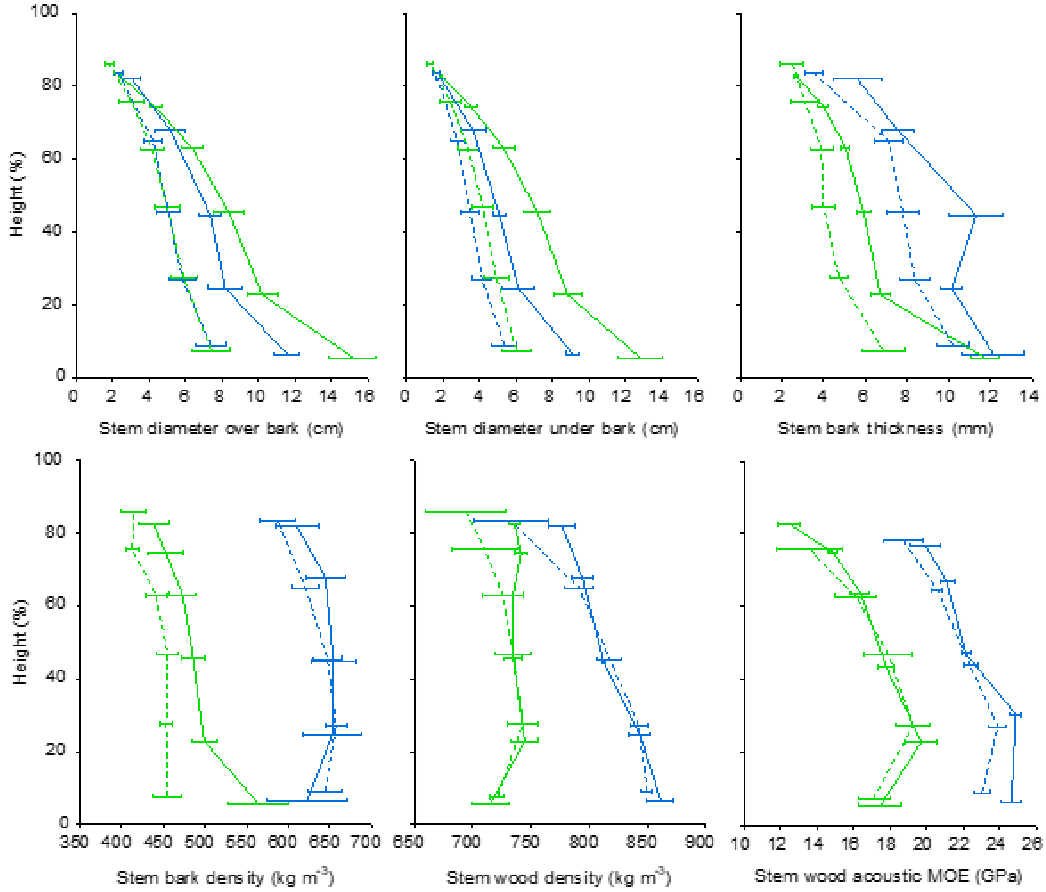
Branch properties of the trees

The branches of the *R. stylosa* trees had similar slenderness, but smaller diameter, and thicker bark, compared with *B. gymnorrhiza* ($P < 0.01$) (Table 3). Thickness of the bark declined along the length of the large and small diameter branches of *B. gymnorrhiza* (Figure 6). The bark was much thicker at the base of the large diameter branches of *R. stylosa* ($P < 0.01$), but for the small diameter branches there was little change in bark thickness along the length of the branches.

Bark density of the branches was higher for *R. stylosa*, compared with *B. gymnorrhiza* ($P < 0.01$) (Table 3). There was little change in bark density along the length of the *B. gymnorrhiza* branches, but the bark density declined along the *R. stylosa* branches, with higher

TABLE 3: Properties of the sampled *B. gymnorrhiza* and *R. stylosa* trees. Mean and range of individual tree, stem, branch and root values in brackets. Different letters indicate significant differences in mean values between species ($P < 0.05$).

Tree properties	*B. gymnorrhia*		*R. stylosa*	
Tree diameter at breast height (cm)	8.5	(4.1-13.0)a	6.6	(3.6-8.9)a
Tree height (m)	5.2	(4.0-6.9)a	5.3	(3.9-6.8)a
Tree depth of live crown (m)	**3.8**	**(2.7-5.1)a**	**2.1**	**(1.3-3.1)b**
Tree branch basal diameter (cm)	**1.9**	**(0.3-5.1)a**	**1.6**	**(0.4-7.3)b**
Stem slenderness	**77**	**(61-110)b**	**109**	**(84-144)a**
Stem bark thickness (mm)	**7.1**	**(4.0-9.7)b**	**9.3**	**(6.9-11.5)a**
Stem bark density (kg m^{-3})	**489**	**(437-544)b**	**641**	**(598-693)a**
Stem wood density (kg m^{-3})	**730**	**(695-747)b**	**836**	**(822-850)a**
Stem wood dynamic MOE (GPa)	**18.1**	**(16.3-20.1)b**	**23.2**	**(21.7-24.3)a**
Branch slenderness	**61**	**(29-101)a**	**59**	**(32-91)a**
Branch bark thickness (mm)	**2.3**	**(1.4-3.5)b**	**3.2**	**(1.3-5.9)a**
Branch bark density (kg m^{-3})	**477**	**(399-587)b**	**612**	**(521-713)a**
Branch wood density (kg m^{-3})	714	(605-761)a	709	(611-786)a
Branch wood dynamic MOE (GPa)	11.7	(8.0-14.1)a	11.8	(6.2-17.3)a
Root bark thickness (mm)	**6.6**	**(4.1-10.5)b**	**8.1**	**(3.0-11.8)a**
Root bark density (kg m^{-3})	**205**	**(159-285)b**	**319**	**(246-440)a**
Root wood density (kg m^{-3})	**516**	**(453-562)b**	**711**	**(610-801)a**
Root wood dynamic MOE (GPa)	**8.1**	**(2.4-12.4)b**	**14.8**	**(9.3-19.8)a**



Tree stem basal diameter: --- *B. gymnorrhiza* <10 cm; —— *B. gymnorrhiza* ≥10 cm;
--- *R. stylosa* <10 cm; —— *R. stylosa* ≥10 cm

FIGURE 4: The tree stem diameter, bark and wood properties at different heights (as a % of height) in the *B. gymnorrhiza* and *R. stylosa* trees. Mean values for tree stems of basal diameter ≥10 cm and <10 cm. The error bars are the standard errors of the means.

bark density at the base of the large diameter branches ($P < 0.05$) (Figure 6).

Wood density and dynamic MOE were similar in the branches of *B. gymnorrhiza* and *R. stylosa* (Table 3). They declined along the length of the branches, and were higher in the large diameter branches ($P < 0.05$), with larger differences occurring between the small and large diameter branches of *R. stylosa* (Figure 6).

The proportion of bark and wood differed in the branches of the two species, with the branches of *B. gymnorrhiza* having a lower proportion of bark, and a higher proportion of wood, compared with *R. stylosa* (Figure 7). Along the length of the branches, the proportion of bark increased in *B. gymnorrhiza*, but remained unchanged in *R. stylosa*.

TABLE 4: Wood properties of the small clears cut from the breast height (1.3 m) stem billets of the sampled *B. gymnorrhiza* and *R. stylosa* trees. Mean and range of individual small clear values in brackets. Different letters indicate significant differences in mean values between species ($P < 0.05$).

Wood properties	*B. gymnorrhiza*		*R. stylosa*	
Moisture content (%)	**13.5**	**(12.7-14.7)a**	**12.2**	**(12.1-12.4)b**
Density (kg m^{-3})	**769**	**(742-815)b**	**910**	**(880-958)a**
Dynamic MOE (GPa)	**12.3**	**(9.3-18.3)b**	**15.9**	**(14.1-17.6)a**
Static bending MOE (GPa)	15.6	(12.6-20.7)a	17.6	(17.0-18.1)a
Static bending MOR (MPa)	151	(131-175)a	176	(170-183)a
Compression strength (MPa)	**56.7**	**(37.0-69.6)b**	**73.8**	**(69.7-77.7)a**
Hardness (kN)	**10.1**	**(9.0-11.6)b**	**13.2**	**(11.9-14.7)a**

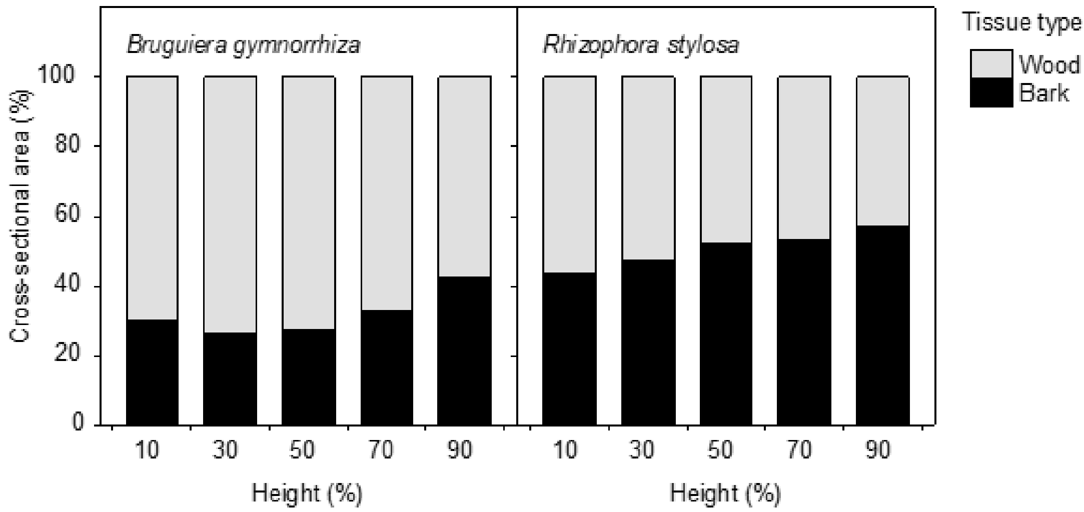
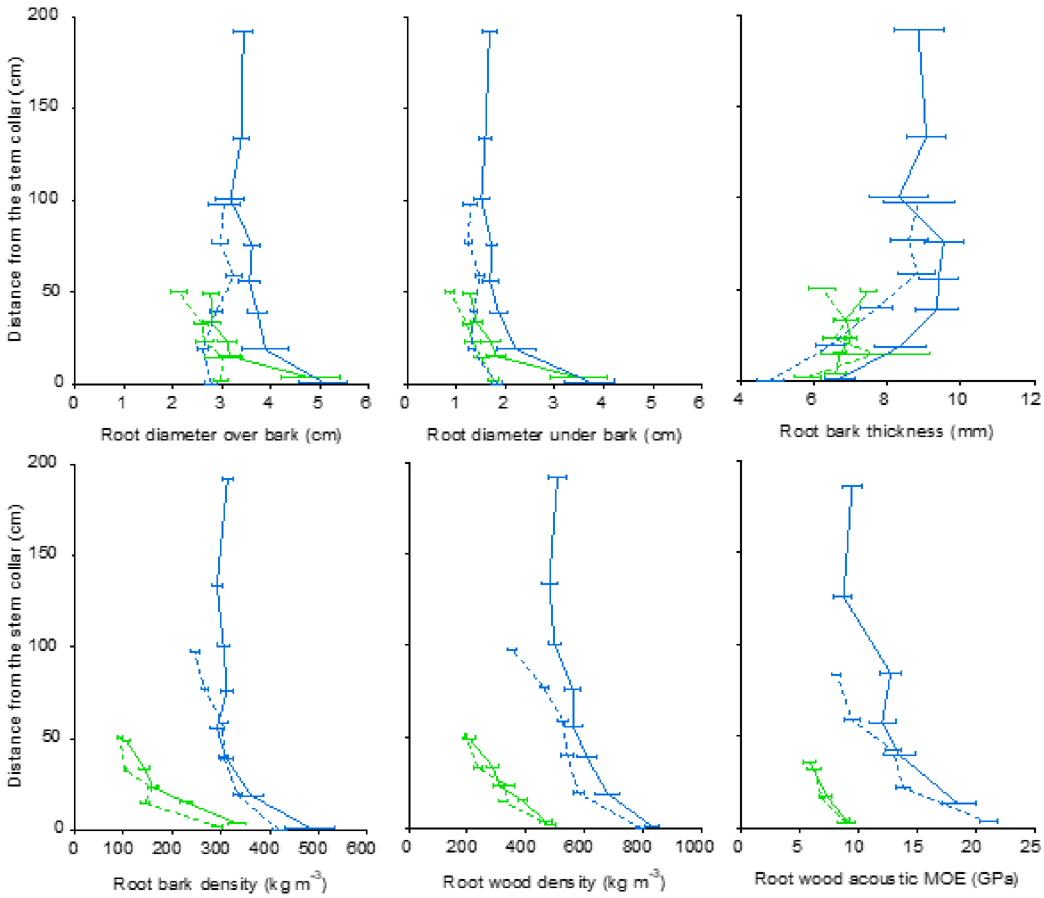


FIGURE 5: The cross-sectional proportion of bark and wood in the tree stems, with height in the *B. gymnorrhiza* and *R. stylosa* trees.

The branches and stems of *R. stylosa* had similar bark density, and the branches and stems of *B. gymnorrhiza* had similar bark and wood density (Table 3). In contrast, the branches had lower wood density than the stems in *R. stylosa*, and the branches had lower wood dynamic MOE than the stems in both *R. stylosa* and *B. gymnorrhiza*.



Branch basal diameter: *B. gymnorrhiza* <2 cm; *B. gymnorrhiza* ≥2 cm; *R. stylosa* <2 cm; *R. stylosa* ≥2 cm

FIGURE 6: The branch diameter, bark and wood properties along the length of the branches (as a % of total length) of the *B. gymnorrhiza* and *R. stylosa* trees. Mean values for tree branches of basal diameter ≥2 cm and <2 cm. The error bars are the standard errors of the means.

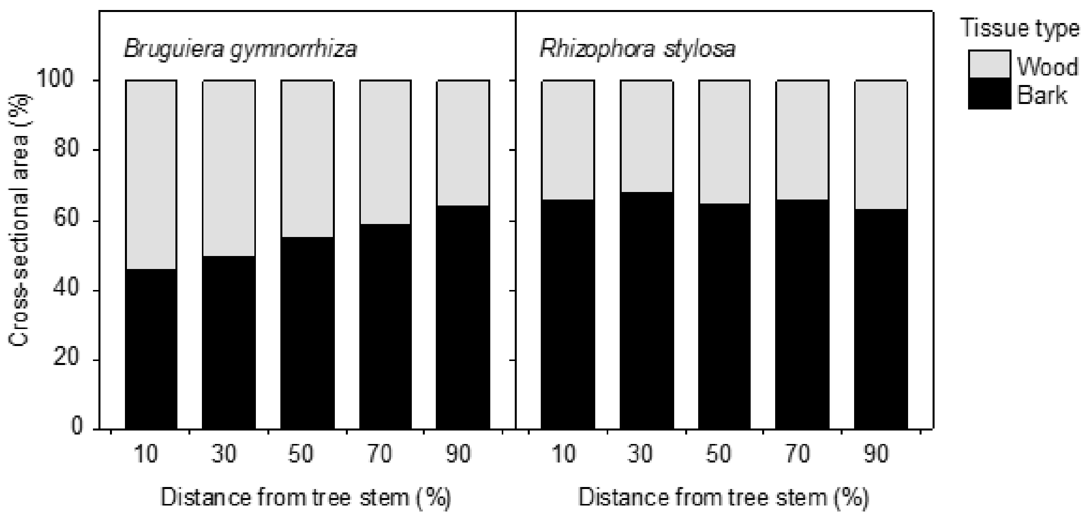
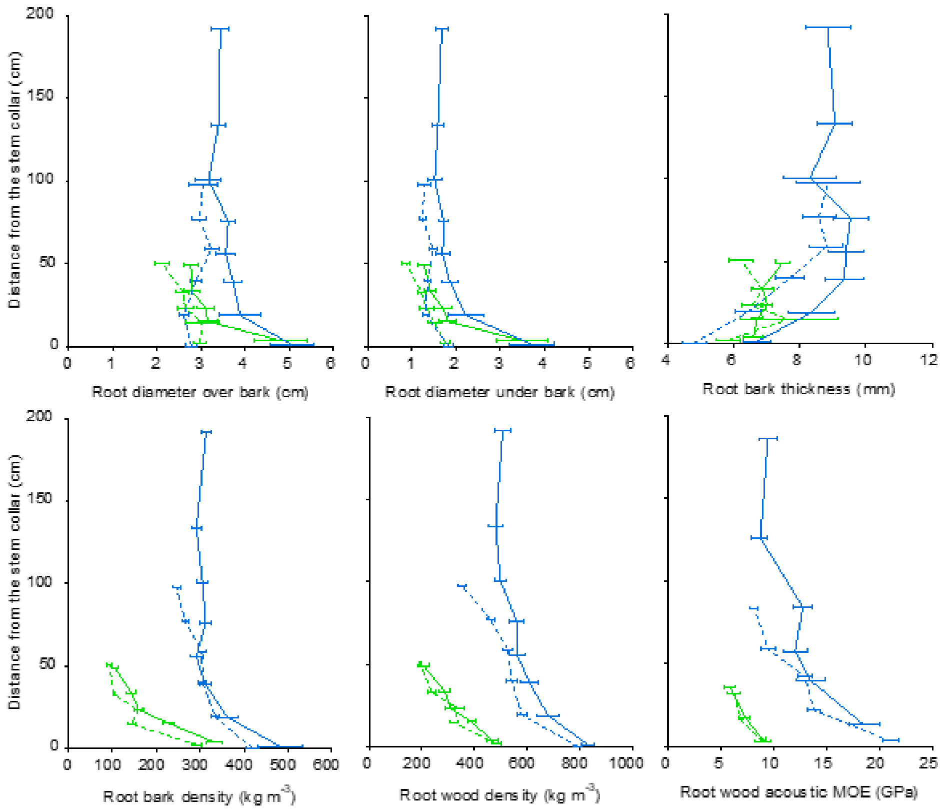


FIGURE 7: The cross-sectional proportion of bark and wood in the branches, with distance from the stem collar, in the *B. gymnorrhiza* and *R. stylosa* trees.

Root properties of the trees

The *R. stylosa* trees formed branched, looping aerial prop roots that arose at intervals along the lower stem, whereas the *B. gymnorrhiza* trees formed stilt roots from the base of the stem, that become shallow buttresses in the older trees.

The roots of both species had similar basal diameter at the tree stem collar, that declined quickly with distance from the stem (Figure 8). Roots of *B. gymnorrhiza* showed a steeper decline in diameter, over a distance of 0.5 m from the stem. At distances of 0.5 to 2.0 m from the stem, the root diameter was unchanged in *R. stylosa*.



Root basal diameter: *B. gymnorrhiza* <4 cm *B. gymnorrhiza* ≥4 cm
R. stylosa <4 cm *R. stylosa* ≥4 cm

FIGURE 8: The root diameter, bark and wood properties with distance from the stem of the *B. gymnorrhiza* and *R. stylosa* trees. Mean values for tree roots of basal diameter ≥4 cm and <4 cm. The error bars are the standard errors of the means.

Bark thickness of the roots increased in both species, over a distance of 0.5 m from the stem (Figure 8). The roots of *B. gymnorrhiza* showed a small increase in bark thickness, but in *R. stylosa* there was a large increase in bark thickness. At distances of 0.5 to 2.0 m from the stem, the root bark thickness was unchanged in *R. stylosa*.

The eccentricity of the *B. gymnorrhiza* and *R. stylosa* roots declined with distance from the stem (Figure 9). Eccentricity of the root wood was greater for the large diameter roots of *B. gymnorrhiza* ($P < 0.01$), and declined gradually with distance from the stem. In *R. stylosa*, the eccentricity was similar for the large and small diameter roots, and declined rapidly to 0.2 m distance from the stem, and then showed little change to 1.0 m distance.

Bark and wood density, and wood dynamic MOE of the roots were higher in *R. stylosa*, compared with *B. gymnorrhiza* ($P < 0.01$) (Table 3). In both species, the bark and wood density, and wood MOE, declined over a distance of 0.5 m from the stem (Figure 8). At distances of 0.5 to 2.0 m the bark density was unchanged in *R. stylosa*, and the wood density and MOE declined slightly.

The proportion of bark was similar in the roots of the two species, but *B. gymnorrhiza* had a lower proportion of wood, and a higher proportion of pith, compared with *R. stylosa* (Figure 10). In both species, the proportion of bark increased, and wood decreased with distance from the stem. Similar trends were observed in the progression from the first to second and third order roots of both species (Figure 11).

The roots had lower bark density than the stems and branches in *R. stylosa* and *B. gymnorrhiza* (Table 3). In *B. gymnorrhiza*, the roots had lower wood density and dynamic MOE than the stems and branches, while in *R. stylosa*, the roots had similar wood density, and higher wood dynamic MOE than the branches, and lower wood density and dynamic MOE than the stems.

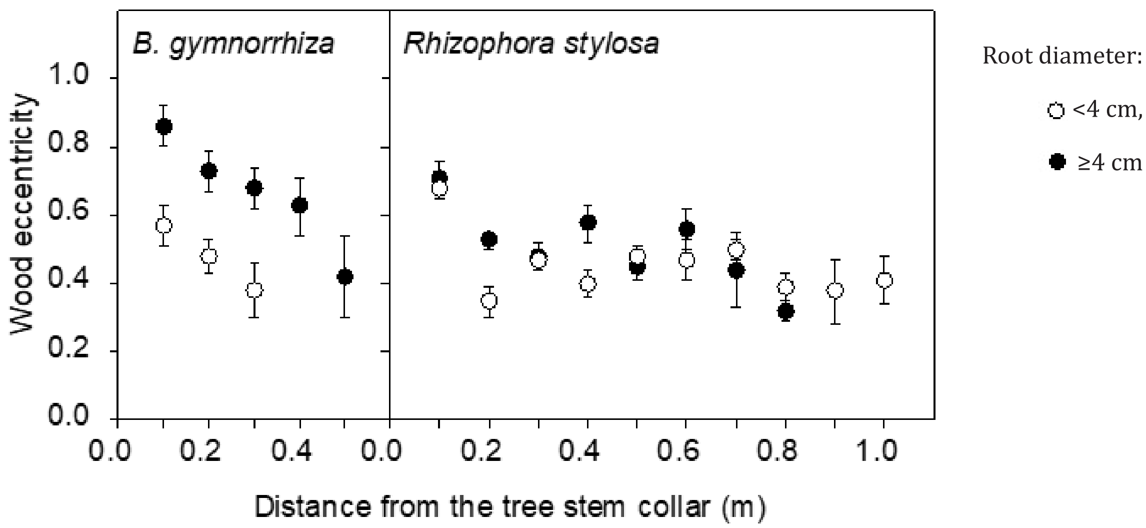


FIGURE 9: Changes in the cross-sectional eccentricity of the wood along the length of the roots of the *B. gymnorrhiza* and *R. stylosa* trees. Mean values for tree roots of basal diameter >4 cm and <4 cm. The error bars are the standard errors of the means.

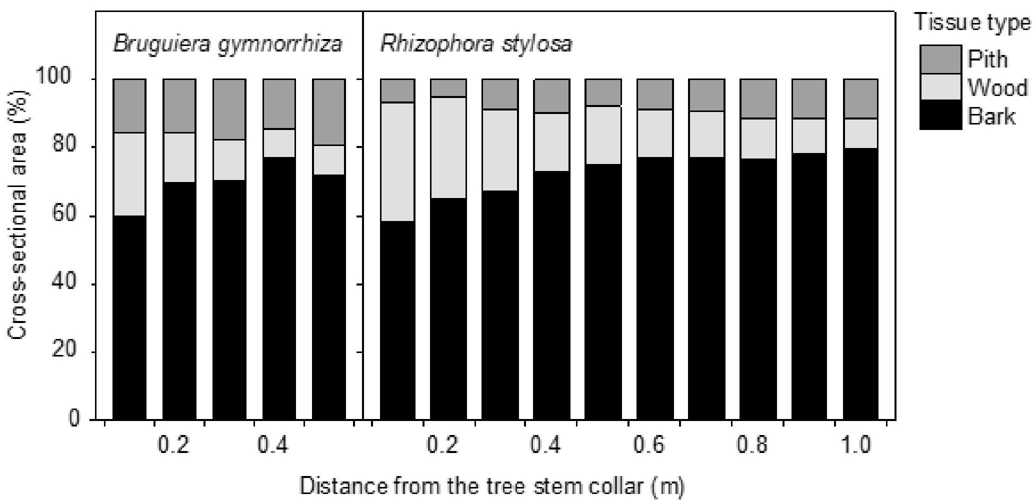


FIGURE 10: The cross-sectional proportion of bark, wood and pith in the roots, with distance from the stem collar of the *B. gymnorrhiza* and *R. stylosa* trees.

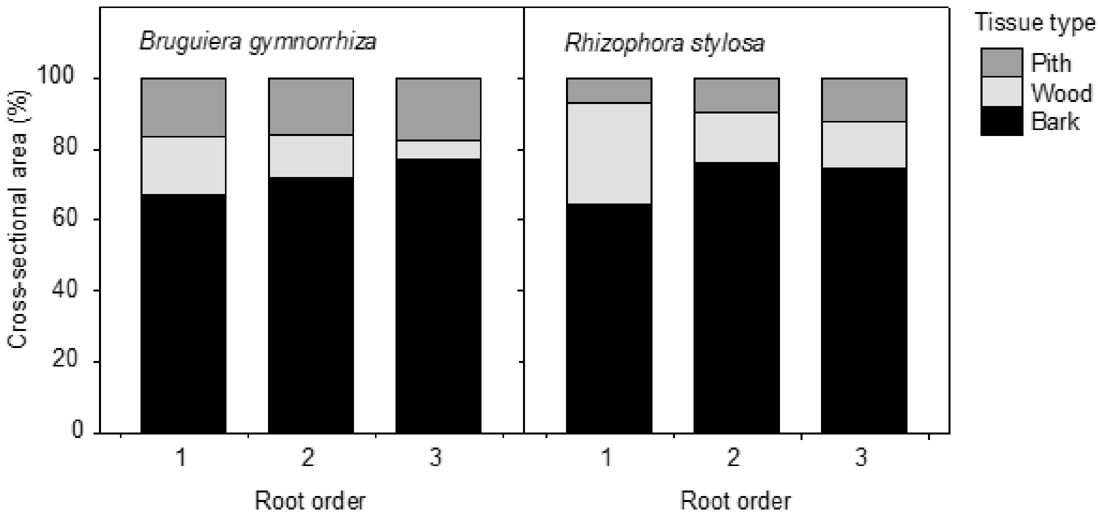


FIGURE 11: The cross-sectional proportion of bark, wood and pith in the first, second and third order roots of the *B. gymnorrhiza* and *R. stylosa* trees.

Discussion

The *R. stylosa* trees in the riverine mangrove forest on Iriomote Island are found in the lower reaches of the rivers, where the stem diameters and growth rates increase towards the riverside, in response to the greater availability of light (Enoki et al. 2009). This exposes the trees to the risk of damage from the action of waves, tidal flows, and wind. The stems of the *R. stylosa* trees have higher wood density and mechanical properties, compared with *B. gymnorrhiza*, that increases their resistance to buckling and rupture, and affords the trees greater protection. It has been observed in tropical forests, that trees with high wood density have lower rates of snapped stems, and are more likely to be undamaged, than trees with lower wood density (Putz et al. 1983; King et al. 2006; Curran et al. 2008; Onoda et al. 2010).

Light demanding tree species produce relatively slender stems, due to the need for height growth to maintain a position in the forest canopy (Poorter et al. 2003). This is seen in the greater slenderness of the stems of *R. stylosa*, which are supported by the aerial prop roots. The greater slenderness makes the stems more flexible, and permits them to bend without breaking (Read & Stokes 2006). Slender stems and high wood density are considered the best combination to provide flexibility and strength to resist strong winds (King 1986; Anten & Schieving 2010).

Woody debris from flooding and storms can cause injuries to mangrove stands (Krauss and Osland 2020). The impact resistance of the bark and wood increases with the density or hardness, due to the increase in the compressive strength perpendicular to the grain, and the absorption of energy by the buckling and collapse of the cell walls (Doyle & Walker 1985; Hepworth et al. 2002). The thicker and higher density of the bark on the stems and branches of *R. stylosa*, and the higher wood density of the stems, provides greater protection from injury caused by woody debris, where this species is dominant at the riverside in the lower reaches of the rivers. Damage to bark can provide an entry for termites and fungal pathogens, and lead to the death of trees (Putz & Chan 1986).

Branches of mangrove trees are more vulnerable to the stresses of waves, tidal flows, and wind, than the stems (Santini et al. 2013). The energy of strong winds is dissipated more effectively in tree crowns with flexible branches, and this results in less strain on the tree stems (Spatz et al. 2007; Spatz & Pfisterer 2013). The mangrove species *B. gymnorrhiza* and *Rhizophora apiculata* Blume have flexible branches, and less stem breakage than *Sonneratia alba* Sm., a mangrove species with stiff branches that are subject to shear (Kauffman & Cole 2010). The slenderness, wood density and dynamic MOE were similar for the branches of *B. gymnorrhiza* and *R. stylosa*. The decline in wood density and dynamic MOE along the length of the branches, will increase the flexibility of the peripheral branches. This allows them to deflect without producing strains large enough to cause failure, and reconfigure to reduce the drag in the crown (Bertram 1989). *Sonneratia alba* has the capacity to sprout from dormant epicormic tissues, and recover from broken stems, but *B. gymnorrhiza*, *R. apiculata*, and *R. stylosa*, have little or no capacity to sprout from older wood, and depend for survival on the retention of peripheral branches with active buds (Bardsley 1985; Tomlinson 1986; Kauffman & Cole 2010).

Shade-tolerant tree species have a greater depth of crown, and lower photosynthetic light compensation points, than light-demanding species, which allows them to have more leaf layers and maintain a higher leaf area index (Sterck et al. 2001; Poorter et al. 2006). The trees of *B. gymnorrhiza* had a greater depth of crown, and frequently occurred as saplings in the understorey of the riverine mangrove forest. Falling branches and trees are a major cause of damage and death in forests, particularly of understorey saplings (Clark & Clark 1991; Van der Meer & Bongers 1996; King et al. 2006). Shade-tolerant tree species have dense wood to enhance survival, with sapling survival positively related to wood density in rain forest species (Muller-Landau 2004; van Gelder et al. 2006). The stems and branches of *B. gymnorrhiza* had similar wood density, and compared with *R. stylosa*, they had a higher proportion of wood. These traits are likely to reduce the damage from falling branches and trees, and enhance the survival of *B. gymnorrhiza* in the understorey.

Trees of *Rhizophora* species show greater survival and resistance to the hydrodynamic forces of storm surges and tsunami waves, than those of *Bruguiera* species (Yanagisawa et al. 2009). The high strength and stiffness of the aerial prop roots of *Rhizophora* species (Mendez-Alonzo et al. 2015; Zhang et al. 2015), allows the roots to stay intact and the trees to remain upright under hydrodynamic forces, while the trees of *Bruguiera* species are easily uprooted (Woodroffe & Grime 1999; Yanagisawa et al. 2009). The aerial prop roots of *R. stylosa* have thicker bark, and higher bark and wood density, and wood dynamic MOE, and a higher proportion of wood, than the roots of *B. gymnorrhiza*. This gives the compressive buttresses of *R. stylosa* greater impact resistance and rigidity to withstand the compressive loadings of the hydrodynamic forces. The tensile buttresses of *B. gymnorrhiza* have a limited ability to withstand compressive loads, and therefore have less resistance in exposed situations (Vogel 1996). The differences are consistent with the growth of *R. stylosa* at the riverside, and *B. gymnorrhiza* away from the riverside, in the lower reaches of the rivers.

Conclusions

The structural properties of the tree stems, branches and roots of *R. stylosa* and *B. gymnorrhiza* are influenced by the ecology of these species in the riverine mangrove forest. The bark and wood properties of the stems and aerial prop roots of the compressive buttresses of *R. stylosa,* provides greater resistance to wind and hydrodynamic forces, in the exposed tidal positions where this light demanding pioneer species grows. The higher proportion of wood in the stems and branches, and lower proportion of wood in the roots of the tensile buttresses of *B. gymnorrhiza*, reflects the risk of damage from falling branches and trees in the understorey, and the less exposed positions of this shade tolerant gap-phase species. The flexible branches of both species, indicates the similar survival requirement of retaining peripheral branches with active buds.

List of abbreviations

DBH: Diameter at breast height
MOE: Modulus of elasticity
MOR: Modulus of rupture

Competing interests

The authors declare that they have no conflict of interest.

Authors' contributions

TJ and SW designed the study, and collected the data; TJ analysed the data and wrote the manuscript.

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Availability of data and material

The datasets generated during the current study are available from the corresponding author on reasonable request.

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