

Accounting intra-tree radial wood density variation provides more accurate above ground mangrove biomass estimation in the Sundarbans

Md. Qumruzzaman Chowdhury

qumrul-for@sust.edu

Shahjalal University of Science and Technology

Swapan Kumar Sarker

Shahjalal University of Science and Technology

Md. Bishal Ali

Shahjalal University of Science and Technology

Md. Imam Hossain Imran

Shahjalal University of Science and Technology

Anup Datta

Shahjalal University of Science and Technology

Jean-Michel Leban

National Research Institute for Agriculture, Food and Environment

comment

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Abstract

Wood density is an important functional trait used to estimate forest biomass and carbon stocks. Its wider range of variations, such as inter- and intra-specific level, and within tree disparity, repeatedly invoke wood density as a potential source of variation in biomass or carbon estimation. We aim to (i) measure pith-to-bark wood density profiles in major mangrove tree species in the Sundarbans and (ii) quantify the deviation in above ground biomass estimations by comparing the method that ignores wood density variation across the radius. One hundred and fifty wood cores were collected from five widely distributed ecologically distinct mangrove species in three distinct salinity zones (low, medium, and high) in the Bangladesh Sundarbans. Wood density was measured for each 1 cm long wood core segment from pith to bark. Among the three light-demanding species, *Sonneratia apetala* and *Avicennia officinalis* showed a decreasing wood density trend from pith to bark while *Excoecaria agallocha* exhibited an increasing trend. Shade tolerant *Xylocarpus moluccensis* displayed a decreasing wood density trend, whereas the most dominant *Heritiera fomes* unveiled almost less variable wood density values from pith to bark. Albeit wood density varied positively with slenderness ratio, a significant relationship was found only for the shade tolerant species. Shade tolerant species also had a significantly higher mean wood density than light demanders. Wood density was significantly higher at the high saline zone for the studied species, except *S. apetala* and *A. officinalis*. Depending on the species, ignoring radial wood density variation increased deviations in AGB estimations up to ~ 17%. This study suggests for considering radial wood density variations, and their possible site- and species-specific influences to increase the accuracy of mangrove biomass estimations. Furthermore, these preliminary results pave the avenue for a better understanding of wood functional traits in the Sundarbans.

Introduction

Mangroves are carbon-rich ecosystems (Donato et al. 2011), that are distinct from other terrestrial ecosystems because they inhabit in saline intertidal habitats in the (sub) tropics (Spalding and Leal 2021). Despite their low species diversity, mangroves are one of the most productive ecosystems on Earth (Ribeiro et al. 2019; Bai et al. 2021). Carbon in mangroves, also known as 'blue carbon', is primarily stored in vegetation and soil (Nellemann and Corcoran 2009; Simard et al. 2019). However, due to rapid environmental changes, land conversions, overexploitation, and die-offs mangroves are shrinking globally ($1-2\% \text{ year}^{-1}$) (Thomas et al. 2017; Goldberg et al. 2020; Bhowmik et al. 2022). Furthermore, increased salinity due to changing climate, including sea level rise (SLR), is degrading mangrove biogeochemistry and hydrology (Ward et al. 2016; Fries et al. 2022), affecting forest structure and functions (Tully et al. 2019; Sarker et al. 2021), and consequently impacting blue carbon sequestration and storage potentials (Lovelock and Ree 2020; Zeng et al. 2021; Ahmed et al. 2023). Understanding the dynamics of mangrove biomass is therefore crucial for setting up carbon financing projects under global mechanisms, such as Reducing Emissions from Deforestation and Forest Degradation (REDD+) and carbon credits under the Paris Agreement (UNFCCC, 2016).

Although mangroves play an important role in global climate regulation by sequestering atmospheric CO₂ in tree biomass (Alongi 2020), accurate estimation of biomass remains a challenge due to uncertainties in quantification (Virgulino-Júnior et al. 2020a; Rahman et al. 2021a) which limits our understanding on their potentials in climate change mitigation. While the choice of allometric model/s remains the main source of uncertainty in biomass estimation (Vorster et al. 2020; Rahman et al. 2021a), potential uncertainties in wood density measurement should not be overlooked because it has a significant influence on tree biomass or carbon stocks (Chave et al. 2005; Bastin et al. 2015; Saeb et al. 2022). Wood (basic) density is the ratio of wood dry mass to fresh wood volume, and it is widely used as a key functional trait to integrate tree structure and functions (Chave et al. 2009; Williamson and Wiemann 2010; Momo et al. 2020), as well as biomass estimation (Plourde et al. 2015; Nam et al. 2018; Suwa et al. 2021). Wood density varies greatly in tropical regions, ranging from 0.10 to 1.53 g cm⁻³ (Zanne et al. 2009). A small variation in wood density, on the other hand, has a greater impact on scaling of tree biomass (Gillerot et al. 2018; Saeb et al. 2022). There is a growing interest in understanding mangrove wood because an accurate estimate of biomass is required to quantify their role in the global carbon cycle.

Basic wood density (henceforth, wood density) varies from individual to community level due to variation in tree growth, age, genetics and environmental factors (Muller-Landau 2004; Williamson and Wiemann 2010; Marra et al. 2014; Ramanananantoandro et al. 2016; Philips et al. 2019). Soil salinity, siltation, and inundation are additional regulatory drivers of wood density variation in mangroves when compared to upland ecosystems (Santini et al. 2012; Virgulino-Jnior et al. 2020b; Sarker et al. 2021). It also varies substantially within a tree, both axially (Wassenberg et al. 2014; Demol et al. 2021) and radially (Nock et al. 2009; Bastin et al. 2015). This variation is also linked to shade tolerance of tree species. For example, the production of low-density wood in many light demanding tree species during the juvenile stage aids in height growth, which is beneficial for capturing competitive light resources (Reich et al. 2014; Pretzsch et al. 2018) although this can shorten life-span of trees (Wiemann and Williamson 1988; Chave et al. 2009; Osazuwa-Peters et al. 2014). Many shade-tolerant species, on the other hand, produce high density wood and survive longer in the understory despite being subjected to different stresses (Lawson et al. 2015). Furthermore, wood density variation is related to mechanical stability (slenderness ratio) of trees (Karlinasari et al. 2021). Higher wood density provides greater resistance to physical damages and biodegrading agents (Chave et al. 2009), increases safety in xylem hydraulic traits (McCulloh et al. 2011; van der Sande et al. 2019) and reduces the metabolism costs (Markesteijn et al. 2011; Fournier et al. 2013). However, wood density variation in mangroves is diminutively known compared to other ecosystems (Santini et al. 2012; Virgulino-Júnior et al. 2020). It is therefore crucial to understand how wood density vary in multiple mangrove species growing under contrasting habitat conditions. This will allow us to better understand and estimate the biomass and carbon in addition to their ecology.

Sundarbans (~ 10,000 km²), the largest solo chunk of mangrove on Earth, supports livelihoods of > 7.5 million climate affected people in the South Asia (Chowdhury et al. 2023a) and provides a low-cost nature-based (NbS) solution for coastal protection (Dasgupta et al. 2020). It also co-benefits biodiversity

conservation including globally endangered plant and animal species (Sarker et al. 2019), and sinks atmospheric CO₂ (Rahman et al. 2021b). Being a Ramsar Wetland Site and a UNESCO World Heritage Site (Gopal and Chauhan 2006), this sentinel mangrove is threatened by anthropogenic disturbances as well as global climate and environmental changes (Sarker et al. 2021; Ahmed et al. 2022). Furthermore, the ecosystem occupies a number of distinct gradients of soil salinity and nutrients (Ahmed et al. 2023), which have a direct impact on biomass production and carbon storage (Rahman et al. 2015, 2021a). Because of growing global concern about blue carbon, the Sundarbans has gained traction for biomass estimation (GOB 2019). Until now, biomass estimates in this ecosystem have primarily relied on plot level mean wood density (without considering the entire radius) or mean wood density from global repositories (Mahmood et al. 2019; Rahman et al. 2015, 2021a, b). However, using single-mean wood density (e.g., mainly outer portion of the stem) data from sample plots ignores the variation of whole stems that might be erroneous due to within tree density variation, which may increase variability in biomass/carbon estimations.

Although mangroves are considered as species poor ecosystems (having only ~ 70 vascular plant species globally; Tomlinson 1986; Duke 2017), the Sundarbans has ~ 50% of them (Aziz and Paul 2015; Mahmood et al. 2019). In this study, we investigate how wood density vary across the radius of each sampled tree and how this variation influence biomass estimation in five widely distributed tree species in the Bangladesh Sundarbans. *Sonneratia apetala* Buch. - Ham. and *Avicennia officinalis* L. are the two light demanding tree species that grow primarily in Indo-Malaysian (IM) and West Pacific (WP) zones (Reef and Lovelock 2015). *Excoecaria agallocha* L., another light demanding species grows naturally throughout the Indo-West Pacific (IWP) zone (Reef and Lovelock 2015). Shade bearing *Xylocarpus moluccensis* Pierre grows in the West Pacific (WP) and *Heritiera fomes* Buch. - Ham. grows in Indo-Malaysian (IM) zone. Historically, these are dominant mangrove tree species in the Sundarbans. However, recent studies (Polidoro et al. 2010; Sarker et al. 2016; 2019) showed that their geographic distributions, populations and carbon storage capacity are declining both in the Sundarbans and globally. A better understanding on biomass dynamics of different species is therefore fundamental to formulate effective forest management plan for the Sundarbans. Therefore, we aim (i) to measure pith-to-bark wood density profiles in five major mangrove species with distinct light characters in three contrasting (low, medium and high) salinity zones in the Bangladesh Sundarbans, and (ii) to quantify the difference in biomass estimations by comparison with the method that ignores within tree wood density variations.

Materials and methods

Study area description

The study was conducted in the Bangladesh Sundarbans that lies in the coast of Bay of Bengal (21° 30′ – 22° 30′ N, 89° 00′ – 89° 55′ E; Fig. 1). Of its total area (6017 km²), about 69 % is land and the remaining areas are waterbodies, such as rivers, small channels and creeks (Wahid et al. 2007). It is inundated regularly twice in a day by high tides and the inundation level varies due to varying elevation and tide levels. The regional hydrology and salinity are regulated by the water enter into the Sundarbans for the

sea (the Bay of Bengal) and the Gorai river. The salinity varies spatially and temporally within the ecosystem (Siddique et al. 2021). Based on the spatial salinity variation, the ecosystem is divided into three salinity zones (Sarker et al. 2019), such as low saline zone (LSZ), mid saline zone (MSZ) and high saline zone (HSZ). Salinity also varies substantially between the seasons. For example, salinity drops due to higher monsoonal (June – September) precipitation and freshwater flows from the upstream rivers (Chowdhury et al. 2016a). Precipitation in the study areas decreases during winter (December – February) followed by pre-monsoon (March – May), and consequently increases the salinity, particularly in pre-monsoon (Siddique et al. 2021). During the post-monsoon (October – November), salinity is also low, despite lower precipitation and freshwater flows.

The Sundarbans is rich in biodiversity and home to a diverse range of tree species, including the IUCN listed globally endangered tree species *H. fomes* (Sarker et al. 2019). The Sundarbans is a part of the Indo-Malaysian mangrove system (Reef and Lovelock 2015). *H. fomes* is the most dominant and flagship tree species, while *E. agallocha* is the second most dominant tree species in the Sundarbans (Chowdhury et al. 2016a, 2023a). Other important tree species in this mangrove are *S. apetala*, *X. moluccensis*, *Ceriops decandra* (Griff.) Ding Hou, *Amoora cucullate* Roxb., *A. officinalis*, *Bruguiera* sp., *Cynometra ramiflora* L., *Aegiceras corniculatum* (L.) Blanco, *Lumnitzera racemose* Willd., *Rhizophora mucronata* Lamk. and *X. granatum* J. Koenig. Besides a wider range of climbers, creepers, grasses and palms are available. Due to different ecological characters, tree species forms different associations in the Sundarbans which vary across the salinity gradients (Iftekhhar and Snegar 2008; Sarker et al. 2016).

Tree measurements and wood sample collection

In this study, five dominant tree species with varying diameters from two distinct shade tolerance categories (Siddiqi 2001), light-demanding (*S. apetala*, *A. officinalis* and *E. agallocha*), and shade tolerant (*X. moluccensis* and *H. fomes*), were selected for sampling. In the Sundarbans, each species was sampled in three distinct salinity zones (e.g., LSZ, MSZ, and HSZ). In each salinity zone, 10 to 15 trees were selected from each species for wood core collection. Diseased, leaning trees as well as trees near the edges of river, creeks, and trails were excluded from sampling. Tree height (m) was measured using a clinometer (Sunnto PM5-360), and diameter at breast height (DBH) over bark (cm) of each tree was measured by using a diameter tape. Slenderness ratio of tree is defined as the ratio of total height to diameter at 1.3 m above ground (Zhang et al. 2020) was calculated for each sample tree. A total of 150 (10 x 3 x 5) trees were cored at breast height (1.3 m above from the ground level) with an increment borer (4.15 mm diameter, Hagl f, Sweden), and the extracted radial cores were examined to confirm the presence of the pith. To ensure accurate measurement of green volume, wood cores were immediately placed in an airtight container to prevent them from drying out.

(Basic) wood density measurement

The wood cores were cut into 1 cm long pieces from pith to bark. Inner wood was defined as an arithmetic mean of the innermost wood of two consecutive pieces (1cm/piece) from pith and outer

wood as an arithmetic mean of the outermost wood of 2 consecutive pieces (1 cm/piece) from bark (Bastin et al. 2015). The average wood density was defined as an arithmetic mean of all wood segments from pith to bark. The volume of each sample was calculated by measuring the fresh sample with a slide caliper, i.e., $\text{volume} = \pi r^2 h$, where r is radius of the increment core and h is the sample length (Chave et al. 2009). Following that, the oven-dry mass of each wood segment was measured using an oven for 24 hours at fixed temperature of 105° C (Chowdhury et al. 2009). Subsequently, basic wood density (g cm^{-3}) was calculated as the ratio of oven-dry mass to green volume.

Above ground tree biomass estimation

Above ground biomass (AGB) was estimated using previously developed multi-species allometric model for the Sundarbans, as follows (Mahmood et al. 2019):

$$\text{Ln (TAGB)} = a + b \text{ Ln (DBH)} + c \text{ Ln (H)} + d \text{ Ln (WD)} \dots\dots\dots (\text{Eq. 1})$$

where, $a = - 6.7189$,

$b = 2.1634$, $c = 0.3752$,

$d = 0.6895$,

AGB = Total Above-ground biomass (kg),

DBH = DBH (cm),

H = Tree height (m),

WD = Wood density (kg m^{-3}), and

a , b , c , and d are the constants.2019) for accurate AGB estimations, with values of 1.0119, 1.0222, 1.0119, 1.02 and 1.0103 for *S. apetala*, *A. officinalis*, *E. agallocha*, *X. moluccensis* and *H. fomes*, respectively.

Deviations in AGB estimations

AGB calculations differed because different values of wood density were used. The first AGB, for example, was calculated using basic wood density from a repository (Kattge et al. 2011). The second AGB measured in this study was for outer wood basic density, and the third was for inner wood basic density (Bastin et al. 2015). Finally, the reference AGB was calculated using the average basic wood density, which was calculated as mean basic wood density of all segments in each tree from pith to bark. The AGB differences were calculated as follows:

AGB difference_{repository} (%) = 100 * (AGB_{repository} - AGB_{reference}) / AGB_{reference} (Eq. 2) AGB

difference_{outer} (%) = 100 * (AGB_{outer} - AGB_{reference}) / AGB_{reference} (Eq. 3)

AGB difference_{inner} (%) = 100 * (AGB_{inner} - AGB_{reference}) / AGB_{reference} (Eq. 4)

Statistical analysis

The Shapiro-Wilk test was used to check normality of the data. Regression analyses were used to examine the radial wood density trend. The variation in wood density among the species was investigated using the Kruskal-Wallis test, followed by a post-hoc (Dunn's) test. The Wilcoxon test was used to examine differences in average wood density between light and shade tolerant categories. Regression analyses were used to examine the variation in wood density in relation to the slenderness ratio, as well as the relationship between inner and outer wood density. The R platform, version 4.0.5 (R Core Team, 2022) was used for all analyses.

Results

Species-specific radial wood density variation

In the studied species, wood density profiles from pith to bark revealed a negative, positive, and neutral trend (Fig. 2). Although both light demanding species, such as *S. apetala* and *A. officinalis*, showed a negative radial trend, wood density in another light demanding species, *E. agallocha*, increased from pith to bark (Fig. 2). Shade-tolerant *X. moluccensis* showed a decreasing trend of wood density from pith to bark. The most dominant shade tolerant *H. fomes*, on the other hand, exhibited a nearly constant pattern of wood density variation across the radius (Fig. 2). Although wood density had a positive relationship with slenderness ratio in both light demanders and shade tolerant species, only the shade tolerant species had a significant relationship (Fig. 3).

Species, shade tolerance and salinity zone-specific wood density variation

The mean wood density variation was significant among the tree species ($p < 0.05$; Fig. 5A). However, the mean wood density did not vary significantly between *A. officinalis* ($0.63 \pm 0.04 \text{ g cm}^{-3}$) and *X. moluccensis* ($0.66 \pm 0.06 \text{ g cm}^{-3}$), although mean wood density in both species significantly varied from other species. *E. agallocha* had the lowest wood density ($0.42 \pm 0.04 \text{ g cm}^{-3}$) and *H. fomes* had the highest value ($0.77 \pm 0.06 \text{ g cm}^{-3}$). The aggregated mean wood density varied with the shade tolerance nature of the species, and a significantly lower wood density was found in light demanding species than shade tolerant species ($p < 0.05$; Fig. 5B).

Among the salinity zones, the mean wood density in *S. apetala* and *A. officinalis* did not vary significantly ($p > 0.05$; Table 1). On the other hand, *E. agallocha* showed a significantly ($p < 0.05$) higher wood density in HSZ ($0.45 \pm 0.08 \text{ g cm}^{-3}$) although the variation was not significant between MSZ ($0.41 \pm 0.07 \text{ g cm}^{-3}$) and LSZ ($0.39 \pm 0.06 \text{ g cm}^{-3}$). *X. moluccensis* and *H. fomes* also showed a non-significant ($p > 0.05$)

wood density variation between LSZ and MSZ while the mean wood density was significantly higher in HSZ (Table 1).

AGB deviation in relation to wood density variation

In the studied species, inner wood density exhibited a positive ($R^2 = 0.61$) relation with outer wood density though the relationship was not significant ($p > 0.05$; Fig. 5). On the other hand, inner and outer wood density relation to average wood density was significant ($p < 0.05$; Fig. 6). Inner wood density overestimated mean AGB up to ~ 17 % in *E. agallocha* (Table 2). The inner wood density of *X. moluccensis* and *H. fomes* produced the lowest deviation in AGB estimations among the species. Similarly, *E. agallocha* had a higher outer wood derived AGB deviation than the other studied species (Table 2). The repository wood density data (Kattage et al. 2011) underestimated AGB by 7 to 10 % in the studied species (Table 2).

Discussion

Radial wood density variation in relation to shade tolerance characters

The radial wood density trends revealed species-specific pattern of variation among the studied mangrove species in the Sundarbans (Fig. 2). Despite the fact that light demanding species such as *S. apetala* and *A. officinalis* showed a decreasing wood density pattern from pith to bark (Fig. 2A, B), *E. agallocha* showed an increasing trend (Fig. 2C). In an earlier study, Santini et al. (2013) showed a decreasing trend of wood density in light-demanding *A. marina* in Australian mangroves. However, a decreasing radial wood density trend in light demanding mangrove species contradicts the general trend in many tropical terrestrial species (Woodcock and Shier 2002; Nock et al. 2009). Both light demanders (*S. apetala* and *A. officinalis*) are early successional species in the Sundarbans (Siddiqi 2001) and colonize newly accreted barren lands where they may face more wind stress and tidal waves on a regular basis, in addition to other environmental stresses such as salinity and siltation. Higher wood density in light demanding species during the juvenile (early) stage of growth may be advantageous for survival in a newly colonized stressful mangrove environment. Trees may reach more favorable conditions in their mature (later) stage of growth, producing low density wood that may enhance tree growth, as described for tropical terrestrial species (Woodcock and Shier 2002; Nock et al. 2009; Chowdhury et al. 2013). Mid-seral light-demanding *E. agallocha*, on the other hand, may benefit from producing low density wood early in growth because this species tends to regenerate in canopy gaps and low-density wood may allow faster growth rates in light environment (Williamson and Wiemann 2010). This species produces high density wood in the outer part of the trunk in adult stature, which may allow them to achieve required strength for mechanical stability (Hietz et al. 2013; Bossu et al. 2018).

In terms of wood density variation, both shade-tolerant species displayed two distinct radial patterns. *X. moluccensis*, for example, showed a decreasing trend, whereas *H. fomes* revealed a nearly constant

pattern of wood density across the radius (Fig. 2). However, as described for various tropical terrestrial species (Woodcock and Shier 2002; Bastin et al. 2015), a decreasing trend is common in shade tolerant species. The negative wood density trend in shade tolerant species reflects the wood allocation strategy may be due to ontogeny (e.g., Woodcock and Shier 2002; Larjavaara and Muller-Landau 2010). Shade tolerant species produce high density wood in juveniles (e.g., Hietz et al. 2013; Plourde et al. 2015), which can limit tree growth but may be advantageous for survival in the forest understory with low light environment because it reduces the risks of pathogen attacks or mechanical damage due to falling branches (Alvarez-Clare and Kitajima 2007; Lawson et al. 2015). Adult trees have reached the canopy layers and produce low density wood (e.g., Woodcock and Shier 2002; Williamson and Wiemann 2010). However, the most dominant shade tolerant *H. fomes* produces almost homogenous wood density along the radius, indicating that growth does not influence radial wood density variability even they in adult stature.

Slenderness ratio is an indicator of mechanical stability in trees (Zahang et al. 2020) with a lower value of 80 indicating biomechanically stability in trees and a higher value of 100 suggesting low stability that is susceptible to mechanical damages like wind or storms (Slodicak and Novak 2006; Kontogiannia et al. 2011). The slenderness ratios of both light demanding and shade tolerant species are generally within 100, indicating high to moderate stability in the sample trees. The slenderness ratio had no effect on wood density in light-demanding species (Fig. 3). In such cases, increasing tree diameter of light-demanding species may confer structural advantages in a fragile mangrove environment by increasing the second moment of area in the tree trunk to resist bending stresses (e.g., Niklas 1998; Gartner et al. 2004), reducing the likelihood of wind damage (Vogel 1988). Shade-tolerant species, on the other hand, demonstrated a significant positive influence of slenderness ratio on wood density variation (Fig. 3). Increasing density of wood in less stable trees may be beneficial for mechanical support of trees in a stressful mangrove environment.

Although the mean wood density varied significantly among the studied species, the difference between *A. officinalis* and *X. moluccensis* was not significant (Fig. 4A). The aggregated mean wood density of light demanding species was significantly lower than that of shade tolerant species (Fig. 4B). Recent growth studies have also revealed that the growth rate of light-demanding *S. apetala* and *E. agallocha* in the Sundarbans is higher than that of shade bearing *H. fomes* (Chowdhury et al. 2016, 2023a; Rahman et al. 2020; Siddique et al. 2021). This suggests that light demanding species require more carbon allocation for faster growth rates, which may result in lighter wood. Shade-tolerant species, on the other hand, require high carbon allocation in wood construction (high wood density), lowering growth rate to minimize transpiration and extend the functional longevity of organs to persist in saline (stressful) conditions (Poorter et al. 2010; Tomlinson et al. 2014).

Wood density variations in relation to salinity

Even though the mean wood density of the studies species was higher at HSZ, only *E. agallocha*, *X. moluccensis*, and *H. fomes* showed a significant variation (Table 1). However, the difference in mean wood density between LSZ and MSZ was not significant. The variation in wood density among salinity

zones indicates the influence of habitat (such as salinity), as previously described for other mangroves (Virgulino-Jnior et al. 2020). High density wood formation in HSZ may be compensated by a slower growth rate in trees. Earlier studies reported that the growth rate of different mangrove species (e.g., *S. apetala*, *E. agallocha* and *H. fomes*) in HSZ is significantly lower in the Sundarbans (Chowdhury et al. 2016, 2023a; Rahman et al. 2020). Depending on the species, it is assumed that habitats regulatory variables (such as salinity, siltation, inundation), resources (such as nutrients) and forest structure (such as height, dbh, stem density) may influence tree growth (Chowdhury et al. 2023a), triggering wood anatomical adjustments that result in variable wood density in mangrove species.

The studied mangrove species produce denser wood in stressful HSZ, which could be due to anatomical changes as an adaptation mechanism to cope with higher salinity (Schmitz et al. 2007; Robert et al. 2009; Madrid et al. 2014; Jiang et al. 2021). The structure of the xylem tissues varies according to the mechanical and hydraulic demands of trees, which are primarily regulated by local environmental conditions (Robert et al. 2009; de Deurwaerder et al. 2016). Santini et al. (2012) showed that *A. marina* maintains high wood density in low saline conditions by increasing cell wall thickness. Similarly, *A. germinans*'s wood had thinner cell walls in the low saline zone and thicker cell walls in the higher salinity zones (Yáñez-Espinosa et al. 2009). Furthermore, high wood density in mangrove species is associated with low vessel lumen area and small vessel size (Preston et al. 2006; Jacobsen et al. 2009), which may provide hydraulic safety to trees in stressful saline conditions (Robert et al. 2009). Because high osmotic concentrations in saline soil can increase xylem tension forces, resulting in vessel embolisms (Cochard 2006). Water conduction dysfunction caused by embolism reduces water flow, affecting the photosynthetic capacity of trees in Australian mangroves (Lovelock et al. 2005, 2006). Sarker et al. (2021) found a positive response of regulatory variables such as salinity, siltation, and soil pH on wood density in the Sundarbans, although the effect size varies from species to species, implying a substantial growth-survival trade-off in mangrove tree species.

Influences on biomass estimations

Wood density variation occurred at multiple scales in the Sundarbans, owing to radial variations in trees, salinity zone-specific variations, and species-specific differences (Figs. 2 & 4; Table 1), as described for terrestrial tropical forests (Chave et al. 2006; Swenson and Enquist 2007; Nock et al. 2009; Bastin et al. 2015; Phillips et al. 2019). The non-significant relationship ($r^2 = 0.61$; $p > 0.05$; Fig. 5) between inner and outer wood density in the studied species suggests that outer wood density cannot be estimated from inner wood density (and vice versa) when species-specific wood density data across the radius are unavailable. However, because of the significant relationship between inner and outer wood density ($p < 0.05$; Fig. 6), average wood density could be predicted. This also suggested that using mean wood density without taking into account radial variation could propagate AGB deviations. As a result, species with an increasing radial wood density trend overestimate AGB using inner wood density, while species with a decreasing radial wood density trend underestimate AGB. Using inner wood density, the light-demanding *E. agallocha* had the highest AGB deviations ($\sim 17\%$) among the studied species (Table 2).

Similarly, light demanding species had higher AGB deviations (~ 6 to 8%) due to the use of outer wood density than shade-tolerant species (Table 2). Shade tolerant *H. fomes* had the lowest AGB deviations for inner and outer wood density due to constant wood density variation across the radius. Regardless of radial variations, the repository derived wood density (Kattge et al. 2011) produced significant underestimations (7 to 10%) of AGB (Table 2). The existing global repositories may lack detailed salinity zone-specific radial wood density variations, which could lead to AGB estimation errors.

Despite the government's commitment to reduce greenhouse gas (GHG) emissions by 21.85% by 2030 (Smith et al. 2021) in order to meet the SDGs, Bangladesh mangroves are still in the planning stages of participating in global carbon markets through various mechanisms such as REDD+ (GOB 2019). However, estimating tree biomass accurately remains a challenge, particularly in Bangladesh mangroves (Rahman et al. 2021a). Taking into account potential deviations in biomass estimation due to radial variation, salinity zone variation, and/or extrapolating from repositories, the use of species-specific zone-specific radial wood density improves the accuracy of AGB estimates and provides insights into the life-history variations of tree species in the Sundarbans. Wood density also varies axially from base to top (Zobel and van Buijtenen 1989), which may contribute to AGB deviations. Future research should consider axial variations to improve the accuracy of biomass estimates in mangroves. Wood density may also vary from sea to landward directions (Santini et al. 2012), so future sampling should include a broader range of samples and species from sea to landward gradients, particularly using x-ray computed tomography (Freyburger et al. 2009; Jacquin et al. 2017) that permit rapid measurement of the wood density from wood cores.

Conclusions

This study provides insights into the extent, prevalence and significance of wood density variations across the radius, shade tolerance and salinity zones in the Sundarbans for accurate AGB estimations, and a better understanding the carbon dynamics. The light-demanding *S. apetala* and *A. officinalis* had a negative radial wood density trend whereas another light-demanding *E. agallocha* showed an increasing trend. Shade tolerant *X. moluccensis* exhibited a negative pattern of wood density while shade tolerant *H. fomes* showed a constant radial trend across the radius. Shade tolerant species had a significantly higher mean wood density than the light-demanding species. Mean wood density was also significantly higher in HSZ compared to LSZ and MSZ in the studied species except *S. apetala* and *A. officinalis*. AGB estimations without considering species-specific radial gradients increase deviations up to ~ 17% in *E. agallocha*. Species with a consistent radial wood density trend (for example, *H. fomes*) had the smallest differences in AGB estimations. Using species-specific average wood density values from the repository causes up to 10% deviations in biomass estimations in the studied species, and thus, wood density data should be used caution. Apart from radial variation, wood density varies axially from root to shoot, taking into account tree age and size, which is beyond the scope of this study. To improve the robustness of wood density values in the Sundarbans, future studies should incorporate axial variations and a larger number of samples including a wider range of tree age and size from sea to landward direction. This study also suggests that biomass estimation accuracy could be improved by taking into account

multiple patterns of wood density variations and if possible, to link these wood density models with growth and yield models, which is important to predict carbon storage potentials in mangroves.

Declarations

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Authors' contributions

MQC conceived the idea; MQC, SKS, AD, MBA collected the samples and analyzed in the lab; MBA, MIHI analyzed the data; MQC wrote the initial manuscript with significant contribution from MQC, SKS, JML. Finally, all authors read and approved the final manuscript.

Availability of data

The data presented in the article will be available upon on request to the corresponding author.

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Tables

Table 1 Mean wood density variation among the salinity zones in the Sundarbans.

Species	Family	Ecological character	zone	n	Average DBH $\pm$ SD (cm)	Average height $\pm$ SD (m)	Average WD $\pm$ SD (g/cm ³)
<i>S. apetala</i>	<i>Lythraceae</i>	LD	LSZ	9	27.1 $\pm$ 10.3 ^b	14.7 $\pm$ 4.9 ^a	0.52 $\pm$ 0.07 ^a
			MSZ	13	41.8 $\pm$ 7.4 ^a	16.7 $\pm$ 0.72 ^a	0.54 $\pm$ 0.08 ^a
			HSZ	10	22.2 $\pm$ 9 ^b	10. $\pm$ 1.9 ^b	0.56 $\pm$ 0.09 ^a
<i>A. officinalis</i>	<i>Avicenniaceae</i>	LD	LSZ	10	26.6 $\pm$ 10.2 ^a	10.9 $\pm$ 3.4 ^a	0.61 $\pm$ 0.095 ^a
			MSZ	10	19.9 $\pm$ 5.5 ^{ab}	7.4 $\pm$ 0.89 ^b	0.63 $\pm$ 0.07 ^a
			HSZ	12	13.5 $\pm$ 4.7 ^b	6.7 $\pm$ 1.14 ^b	0.65 $\pm$ 0.08 ^a
<i>E. agallocha</i>	<i>Euphorbiaceae</i>	LD	LSZ	15	13.9 $\pm$ 1.2 ^a	7.6 $\pm$ 0.99 ^a	0.39 $\pm$ 0.06 ^b
			MSZ	12	13.96 $\pm$ 2.1 ^a	8 $\pm$ 1.2 ^a	0.41 $\pm$ 0.07 ^b
			HSZ	16	12.4 $\pm$ 3.3 ^a	6.3 $\pm$ 1.2 ^b	0.45 $\pm$ 0.08 ^a
<i>X. moluccensis</i>	<i>Meliaceae</i>	ST	LSZ	14	21.6 $\pm$ 7.1 ^a	9.6 $\pm$ 2.6 ^a	0.63 $\pm$ 0.09 ^b
			MSZ	10	15.5 $\pm$ 7.3 ^a	6.7 $\pm$ 1.5 ^b	0.65 $\pm$ 0.08 ^b
			HSZ	14	15.2 $\pm$ 6.7 ^a	7.04 $\pm$ 1.1 ^b	0.71 $\pm$ 0.03 ^a
<i>H. fomes</i>	<i>Sterculiaceae</i>	ST	LSZ	13	17.3 $\pm$ 5.3 ^a	11.1 $\pm$ 5.1 ^a	0.74 $\pm$ 0.09 ^b
			MSZ	10	14.6 $\pm$ 5 ^{ab}	8.6 $\pm$ 2.14 ^a	0.76 $\pm$ 0.07 ^b
			HSZ	9	11.1 $\pm$ 1.6 ^b	8.1 $\pm$ 1 ^a	0.81 $\pm$ 0.05 ^a

n, number of sample trees

LD, light demander; ST, shade tolerant

LSZ, low salinity zone; MSZ, mid salinity zone; HSZ, high salinity zone

SD, standard deviation; WD, wood density

Different letters indicate the is value is significantly different

Table 2. AGB deviations (%) using inner wood density, outer wood density and repository derived wood density. +, overestimation; –, underestimation.

Species	ABG difference due to inner wood density (%)	ABG difference due to outer wood density (%)	ABG difference due to repository wood density (%)
<i>A. officinalis</i>	- 4.52	+ 6.16	-9.02
<i>E. agallocha</i>	+ 17.21	-8.05	-9.32
<i>S. apetala</i>	- 6.56	+ 7.66	-9.45
<i>X. moluccensis</i>	- 3.90	+ 6.01	-7.27
<i>H. fomes</i>	+ 0.60	- 0.19	-9.95

Figures

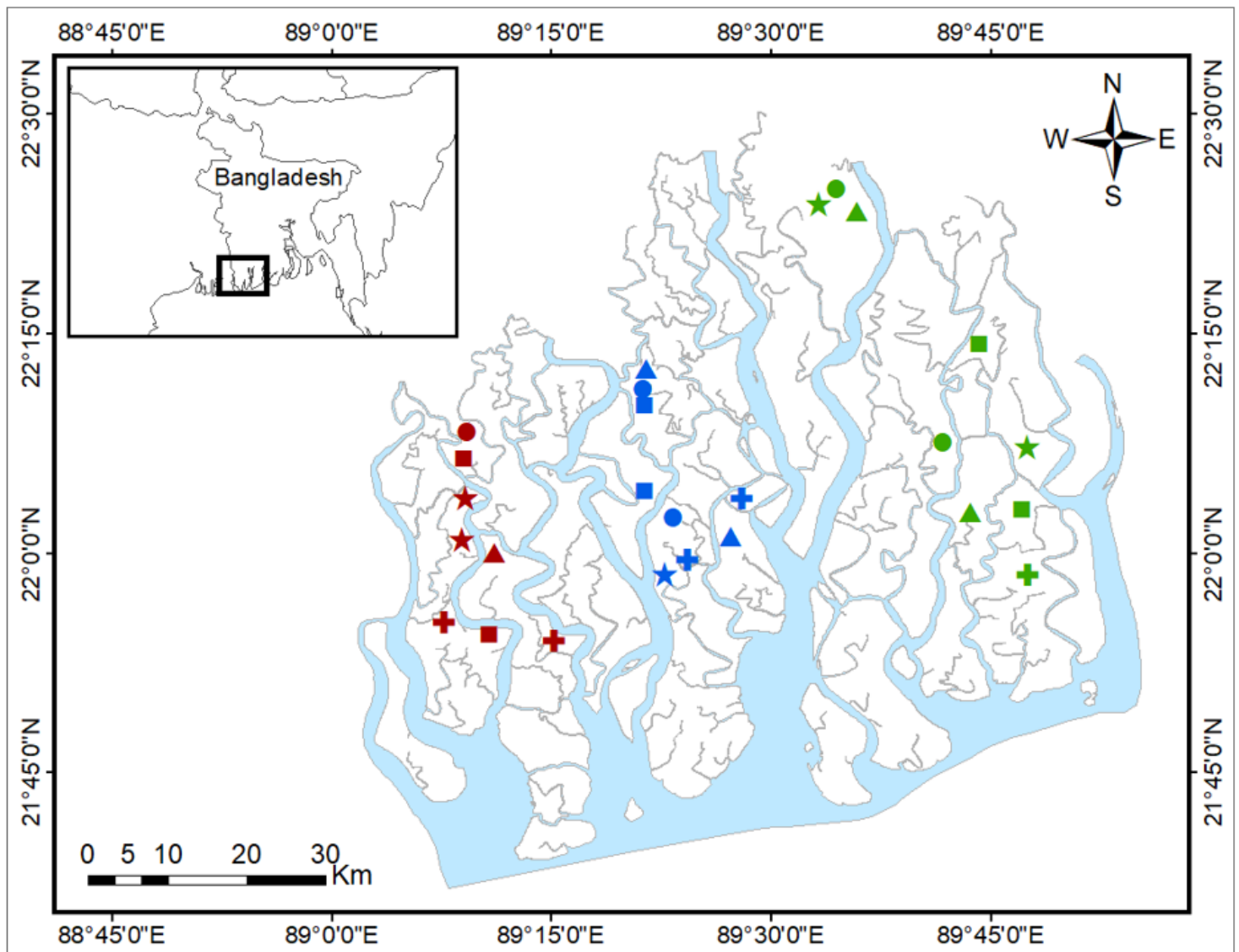


Figure 1

Sampling locations of the studied five species in three different Salinity zones in the Sundarbans. Triangle, *Heritiera fomes*; square, *Xylocarpus moluccensis*; star, *Avicennia officinalis*; Plus, *Sonneratia apetala*; circle, *Excoecaria agallocha*. Green, LSZ; Blue, MSZ; Brown, HSZ.

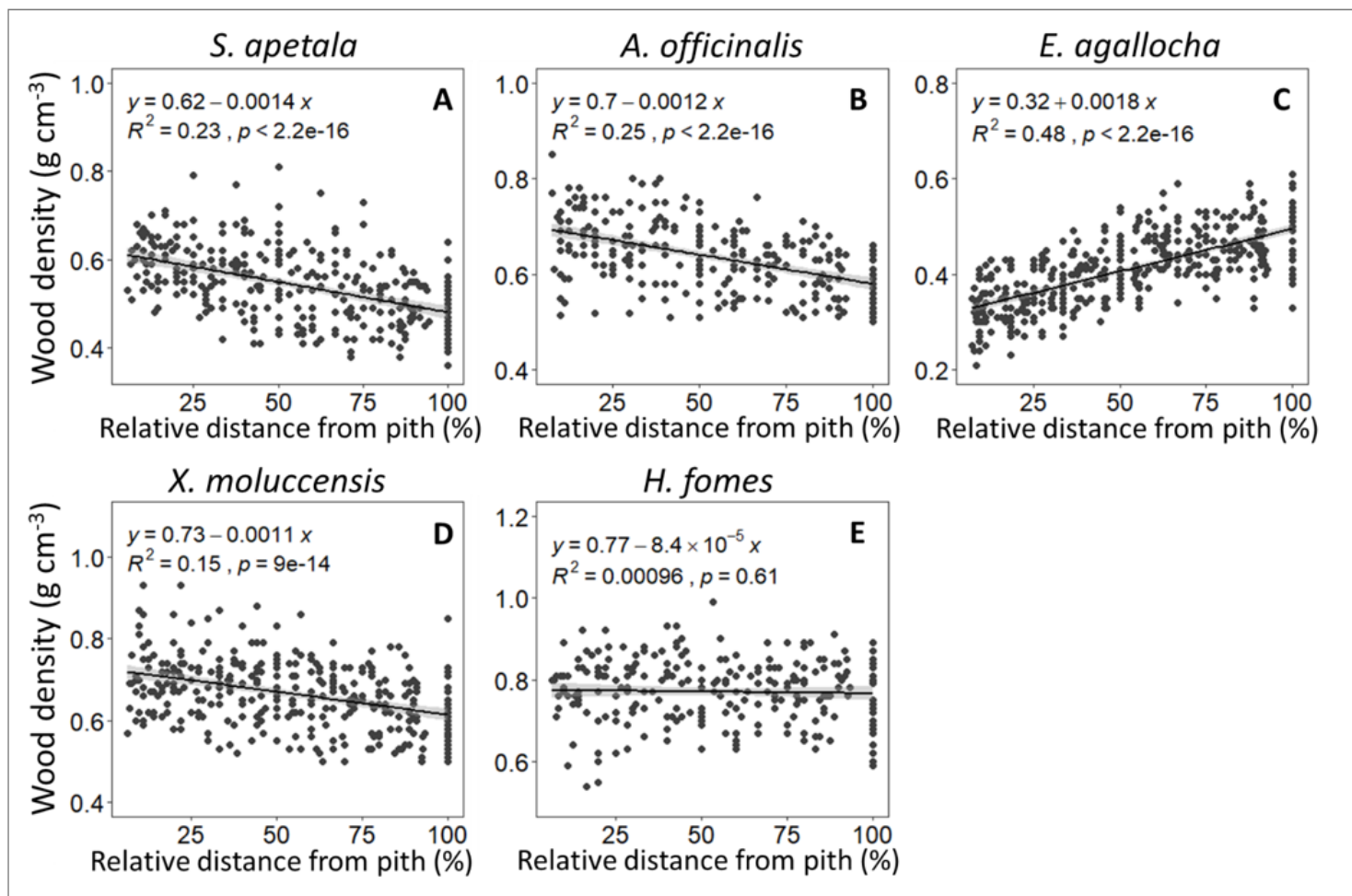


Figure 2

Radial variation of wood density from pith to bark in the studied mangrove species in the Sundarbans.

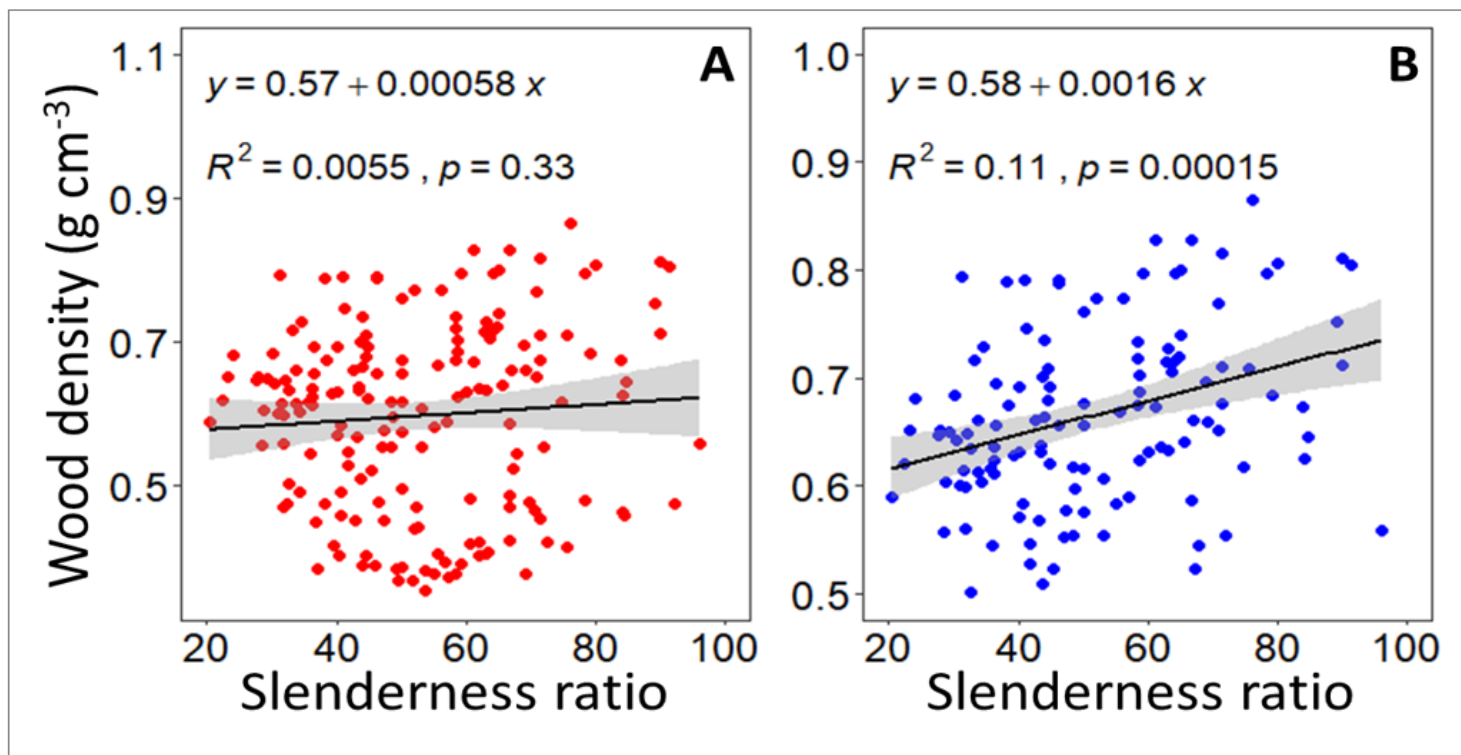


Figure 3

Wood density variation with slenderness ratio in light demanding species (A) and shade tolerant species (B).

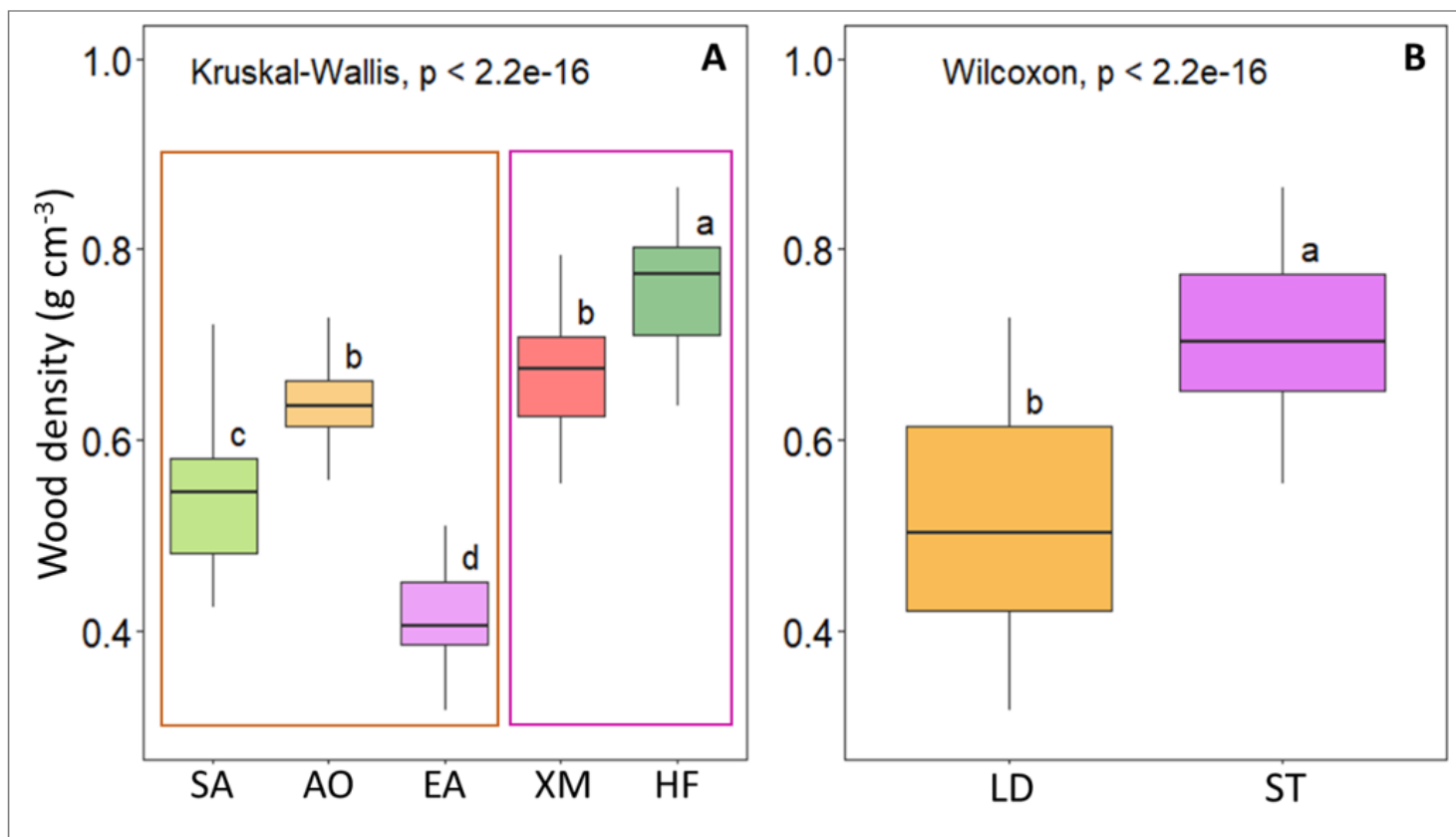


Figure 4

Average wood density variation among the studied species, SA, AO, and EA are light demanding (LD) species and XM and HF are shade tolerant (ST) species (A). Average wood density variation between light demanding (LD) and shade tolerance (ST) category (B). SA, *S. apetala*; AO, *A. officinalis*; EA, *E. agallocha*; XM, *X. moluccensis*; HF, *H. fomes*. Different letters indicate significantly different.

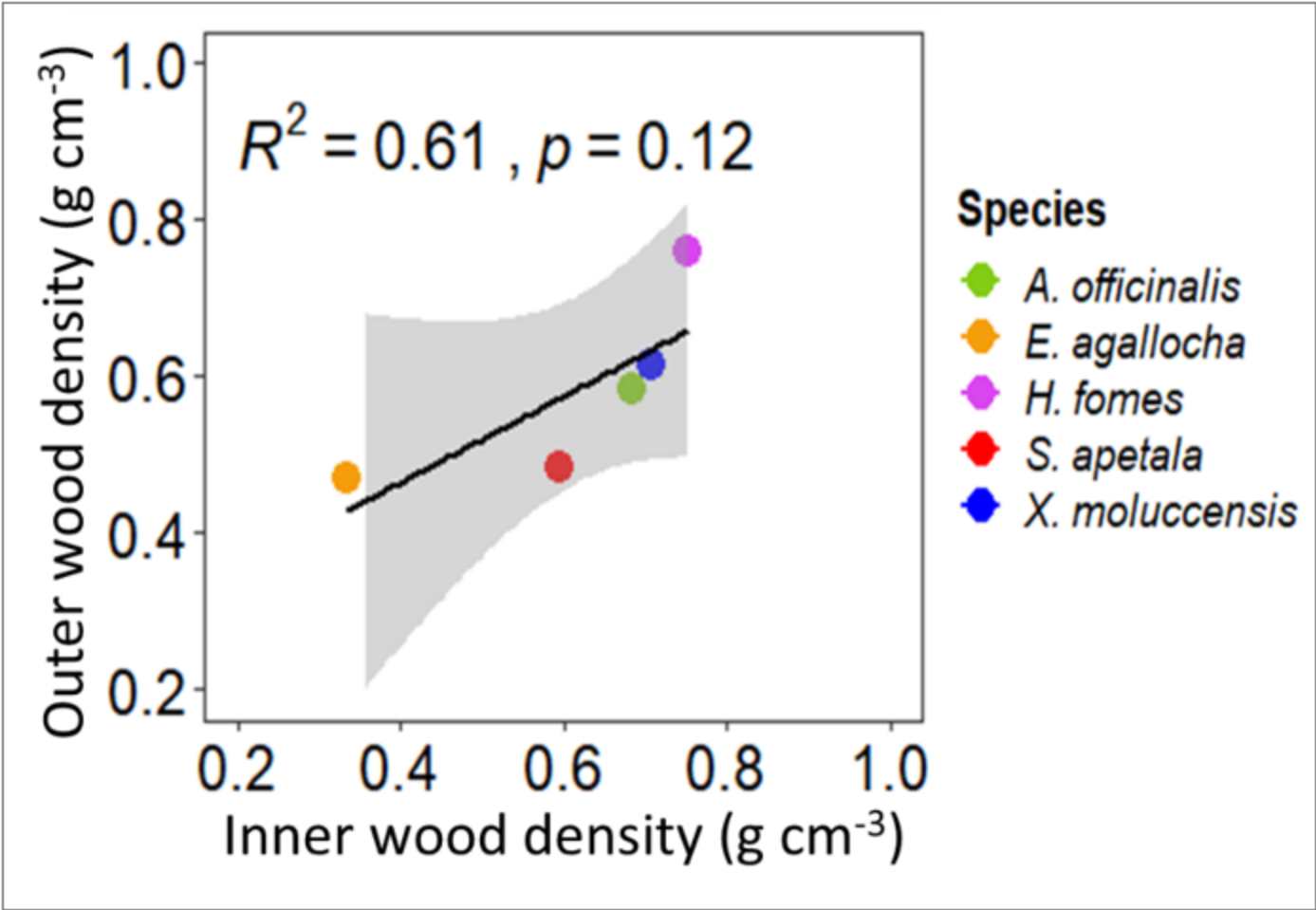


Figure 5

Relationship between outer wood density and inner wood density at species level.

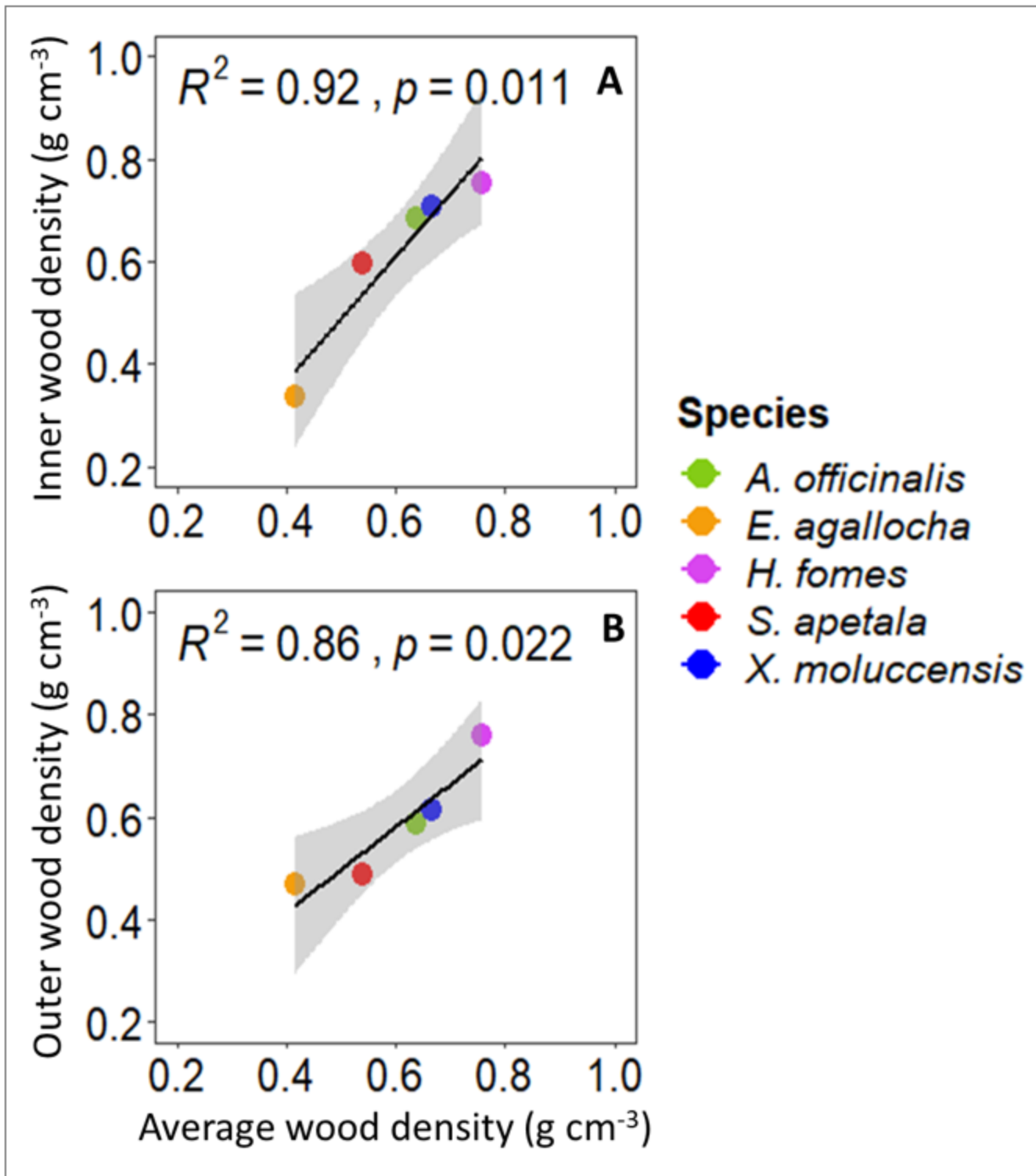


Figure 6

Inner wood density (A) and outer wood density (B) variation with average wood density among the species.