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Wood density and water content in diverse species from lowland dipterocarp rainforest and dry dipterocarp forest

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Abstract We compared the wood density and water content of various tree species in lowland dipterocarp rainforest in Sarawak and dry dipterocarp forest in Cambodia. We collected wood core samples of 134 species from Lambir National Park, Sarawak and those of 44 species from Kratie Province, Cambodia. Sarawak (0.64 g cm^{-3}) and Cambodia (0.64 g cm^{-3}) did not differ in average wood density. In contrast, wood water content in Cambodia (0.42 g cm^{-3}) showed significantly larger values than that in Sarawak (0.35 g cm^{-3}). There was a negative correlation between wood density and water content in Cambodian trees, while the relation was not significant for Sarawak trees. The higher water content in Cambodian trees may indicate the greater importance of stem water storage under the drier environment in dry dipterocarp forest than in lowland dipterocarp rainforest.

Keywords Biomass, Carbon, Dry deciduous forest, Mixed dipterocarp forest, Wood specific gravity

Introduction

Tree woody tissues perform several fundamental functions: they provide biomechanical support for stems that suspend photosynthetic tissues above the ground, they conduct water and nutrients along the soil–plant–atmosphere continuum, and they act as stores for nutrients and water (Chave et al. 2009). Several key traits of woody tissues that relate to tree functional traits such as growth rate, survival and photosynthesis have been proposed in previous research (Santiago et al. 2004; King et al. 2005; Osunkoya et al. 2007; Kenzo et al. 2011; Hiromi et al. 2012). For example, Goldstein et al. (1998) claimed that stem water storage may partially compensate for an increase in axial hydraulic resistance with tree size and thus play an important role in regulating the water status of leaves exposed to the large diurnal variations in evaporative demand that occur in the canopies of seasonal dry tropical forests. Santiago et al. (2004) also found that trees with low wood density tended to have high growth, photosynthetic ability and hydraulic conductance compared with trees with high wood density in Panamanian tropical forest. Wood density is also an important parameter to identify forest biomass (Baker et al. 2004), because coefficients of allometric equations are highly correlated with wood density (Chave et al. 2005, 2014; Komiyama et al. 2005; Kenzo et al. 2009ab). In fact, variations of community-averaged wood density among different forest types were significantly associated with forest biomass in South American tropical forests (Malhi et al. 2006; Saatchi et al. 2007; but see, Stegen et al. 2009), whereas this was not true in Bornean tropical rainforests (Slik et al. 2010). This difference may have been due to the significant domination of Dipterocarpaceae (Slik et al. 2010) and the relatively small variation of climate in the latter compared with South American tropical forests.

Wood properties such as wood density and water content are known to vary depending on the environmental conditions (Sungpalee et al. 2009; Onoda et al. 2010; Fortunel et al. 2012, 2014). Previous reports in neotropical areas showed that forest trees in low precipitation areas had high wood density compared with those in rich rainfall areas (Barajas-Morales 1987; Holbrook et al. 1995; Wiemann and Williamson 2002; Chave et al. 2006; Lohbeck et al. 2013). Slower growth rate of dry tropical forest trees may be a cause of the higher density (Barajas-Morales 1987). In fact, many tree species with low growth rates, such as understory trees, showed higher wood density than fast-growing species such as pioneer species (Suzuki 1999; Muller-Landau 2004). Slik et al. (2010) also found that *kerangas* and peat swamp forest trees with slower growth rates had relatively high wood density compared with lowland dipterocarp forest trees in Borneo. High wood density is also adaptive to dry environments, because trees with high wood density have high tolerance to drought stress with low stem water potential due to having high physical strength with thick cell walls (Holbrook et al. 1995; Onoda et al. 2010). However, variations of wood density among tropical rain forests and dry forests in Southeast Asia have not been well studied compared with those among South American tropical forests (Barajas-Morales 1987; Chave et al. 2006). We hypothesized that tropical dry forests in Southeast Asia might also have high wood density and water content compared with tropical rainforests, because the growth rate of tropical dry forest trees might be limited by the severe dry season and stem water storage might have a substantial role in the mitigation of drought stress under the drier environment. To test this hypothesis, we compared the wood density and water content of lowland dipterocarp rainforest without clear rainfall seasonality in Sarawak and dry dipterocarp forest with severe dry periods in Cambodia.

Materials and Methods

Study sites

Our study was conducted in lowland mixed dipterocarp forest in Sarawak, Malaysia and dry dipterocarp forest (DDF) in Kratie, Cambodia. In Sarawak, we made measurements at a Crane Plot (4 ha) and a Canopy Biology Plot (8 ha) in Lambir Hills National Park (4º20'N, 113º50'E; 150–250 m a.s.l.). The mean height of the canopies of stands was 30–40 m, and some emergent trees reached 50 m in height (Table 1). Tree flora was very diverse and the canopy layer mainly consisted of Anacardiaceae, Dipterocarpaceae, Legminosae, and Sapotaceae. The study sites were in a humid tropical area with no distinct dry season. The annual precipitation at the study site averaged 2600 mm from 2000 to 2009, and the average annual temperature from 2000 to 2009 was 25.8 °C (Kume et al. 2011). The soil type at the site was ultisols.

In Cambodia, we made measurements in a 4 ha plot established in DDF (12°55'N,

Table 1 Annual rainfall, average temperature, soil type, and basal area (BA), maximum tree height, and maximum tree diameter at breast height (DBH) in the research sites in Cambodia and Sarawak, respectively.

Site	Rainfall ($mm\ y^{-1}$)	Average temperature (°C)	Soil type	BA ($m^2\ ha^{-1}$)	Canopy height (m)	Maximum DBH (cm)
Cambodia	1500-1700	26.9	plinthosol	14	10-20	65
Sarawak	2600	25.8	ultisol	33-38	50-70	190

Table 2 Average diameter at breast height (DBH) for sampled trees, and average, minimum and maximum wood density and wood water content in Cambodia and Sarawak, respectively. Asterisks mean significant differences between sites (ANOVA, $P < 0.001$).

		Wood density			Wood water content		
Site	DBH (cm)	Average ($g\ cm^{-3}$)	Min. ($g\ cm^{-3}$)	Max. ($g\ cm^{-3}$)	Average ($g\ cm^{-3}$)	Min. ($g\ cm^{-3}$)	Max. ($g\ cm^{-3}$)
Cambodia	37 ± 2.8*	0.64 ± 0.17	0.42	0.88	0.42 ± 0.1*	0.28	0.60
Sarawak	20 ± 1.9*	0.64 ± 0.16	0.21	0.95	0.35 ± 0.1*	0.15	0.63

106°11'E). Annual rainfall in this region was 1500–1700 mm (Table 1), most of which (approx. 90 %) occurred during the rainy season from May to October (Iida et al. 2015). The vegetation at the study site was classified as typical DDF (Ashton 2014). All tree species shed leaves during the dry season, though leaf phenology significantly varied according to the species (Iida et al. 2015). Most of the canopy trees were 10–15 m high, mainly consisting of Combretaceae, Dipterocarpaceae and Leguminosae. Tall grasses (approx. 1 m in height) and dwarf bamboo (*Vietnamosasa pusilla*, Poaceae) densely covered the forest floor (Kenzo et al. 2014). The surface geology consisted of old sedimentary rocks and terrace gravel, and the soil type was plinthosol according to the FAO classification; the width of the soil layer ranged from 100 to 300 cm (Ohnuki et al. 2008).

Wood core sampling

We collected wood core samples (approx. 5–20 cm in length) using an increment bore (Sungpalee et al. 2009). In total, 291 tree individuals representing 134 species in 34 families from Sarawak and 102 tree individuals representing 44 species in 19 families from Cambodia were sampled. Sampled cores were immediately measured for their fresh weight and volume to calculate water content. These cores were oven-dried at 100 ºC for > 72 h until they reached constant mass. We determined wood density as wood dry mass per fresh volume and wood water content as wood water mass per fresh volume, respectively (Suzuki 1999).

Results and Discussion

Wood density and water content in Cambodia and Sarawak

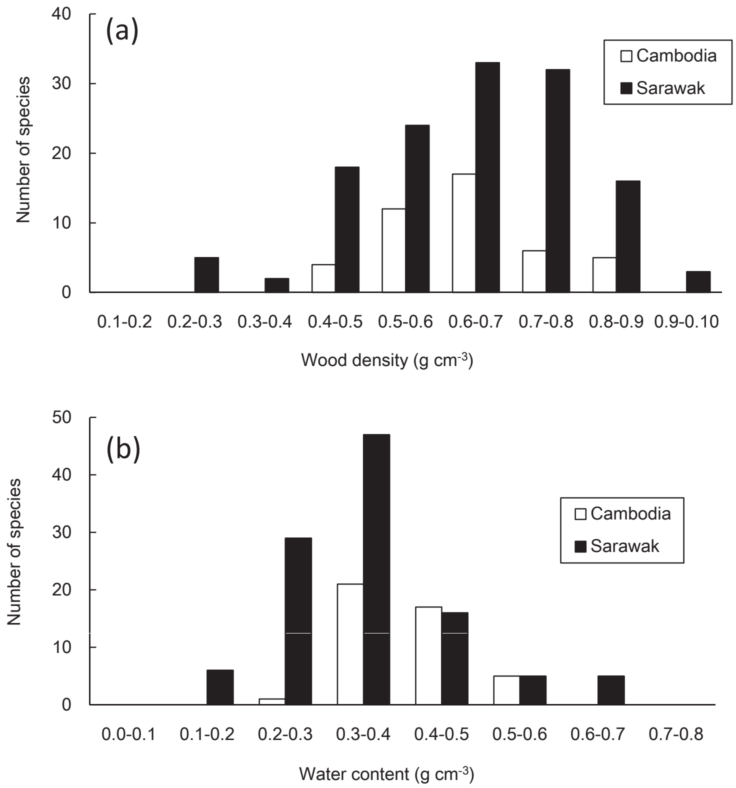

Fig. 1 Histograms of wood density (a) and water content (b) in Cambodia and Sarawak.

The average wood density showed almost the same values in Sarawak and Cambodia (Table 2, 0.64 g cm^{-3}). This similarity between dry and wet tropical forests was not consistent with previous reports from South American tropical rainforests, where wood density usually increased along with decreasing rainfall or the length of the dry spell (Barajas-Morales 1987; Wiemann and Williamson 2002; Chave et al. 2006; Lohbeck et al. 2013). Although a clear reason for the little difference between the two forest types in the present study is unknown, it is maybe related to other environmental factors such as soil conditions. For example, Muller-Landau (2004) claimed that average wood density depended more on soil fertility than on rainfall in several neotropical forests, because soil traits strongly affected the tree growth rate, which affected wood density in turn (Suzuki 1999; Osunkoya 2007). Several researchers also found no relation between mean wood density and rainfall in tropical forests (Williamson 1984; ter Steege and Hammond 2001). Further large datasets on community-level wood density from broad climate zones in tropical Southeast Asia are needed to clearly understand the relation between wood density and environmental conditions, especially rainfall and the dry season.

The average wood density in both forests examined here was generally higher than those of the other forests in Southeast Asia reported so far. Turner (2001) reported that the average wood density in 428 tree species in Southeast Asian was 0.57 g cm^{-3}. The values in lowland dipterocarp forests in West Kalimantan (0.56 g cm^{-3}, Suzuki 1999) and in Brunei (0.59 g cm^{-3}, Osunkoya 2007), and in tropical mountain forests in northern Thailand (0.55 g cm^{-3}, Sungpalee et al. 2009) were also lower than that in the present study. In contrast, Chave et al. (2006) surveyed diverse neotropical tree species (2456 species) in their large survey from Central to South American forests, and reported a very similar value of mean wood density (0.645g cm^{-3}) to that in the present study.

Table 3 Average wood density and water content in major families. Numbers in parentheses indicate species numbers. Asterisks mean significant differences between sites (ANOVA, $P < 0.05$).

Family	Wood density (g cm^{-3})		Wood water content (g cm^{-3})	
	Cambodia	Sarawak	Cambodia	Sarawak
Anacardiaceae	0.49 ±0.04 (4)	0.60 ±0.07 (7)	0.45 ±0.04 (4)	0.26 ±0.02 (7)*
Dipterocarpaceae	0.72 ±0.05 (3)	0.67 ±0.03 (23)	0.42 ±0.04 (3)	0.35 ±0.02 (18)
Euphorbiaceae	0.60 ±0.03 (4)	0.57 ±0.07 (13)	0.42 ±0.03 (4)	0.29 ±0.03 (13)*
Leguminosae	0.66 ±0.04 (9)	0.76 ±0.03 (5)	0.39 ±0.03 (9)	0.33 ±0.05 (3)
Rubiaceae	0.64 ±0.03 (7)	0.55 ±0.13 (3)	0.43 ±0.03 (7)	0.49 ± 0.12 (3)

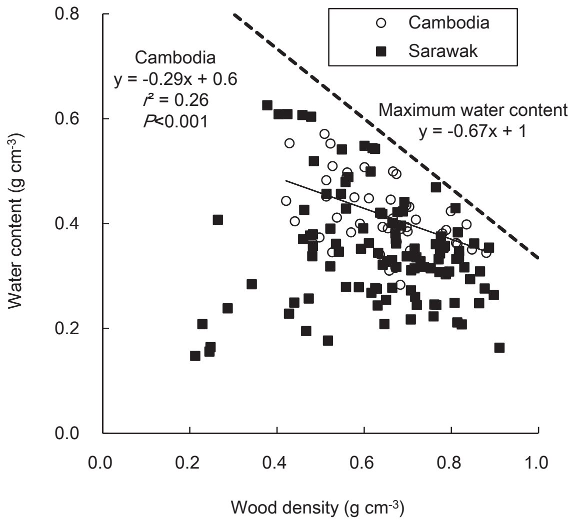

Fig. 2 Relationship between wood density and water content in Cambodia and Sarawak.

We found a wider range of interspecific wood density in Sarawak (0.74 g cm^{-3}) than in Cambodia (0.46 g cm^{-3}, Fig. 1, Table 2). Wider ranges of interspecific wood density in tropical rainforests than in dry forests were also reported in neotropical areas (Williamson 1984). These large interspecific variations may be due to high species-richness with diverse tree functional groups, such as pioneer, understory and canopy trees, in tropical rainforests compared with that of tropical dry forests (Ashton 2014).

In contrast to wood density, a significant difference was found in wood water content between Cambodia and Sarawak. Wood water content was higher in dry dipterocarp forest in Cambodia than in tropical rainforest in Sarawak (Fig. 1, Table 2). We also found high water content in dry dipterocarp forest in several major families, except for Rubiaceae, in which the number of species sampled was relatively small (Table 3). Ecophysiological studies indicated that water storage in the stem mitigates severe drought stress on both diurnal and annual scales in tropical trees, especially in dry tropical forests (Holbrook et al. 1995). Stem water is also

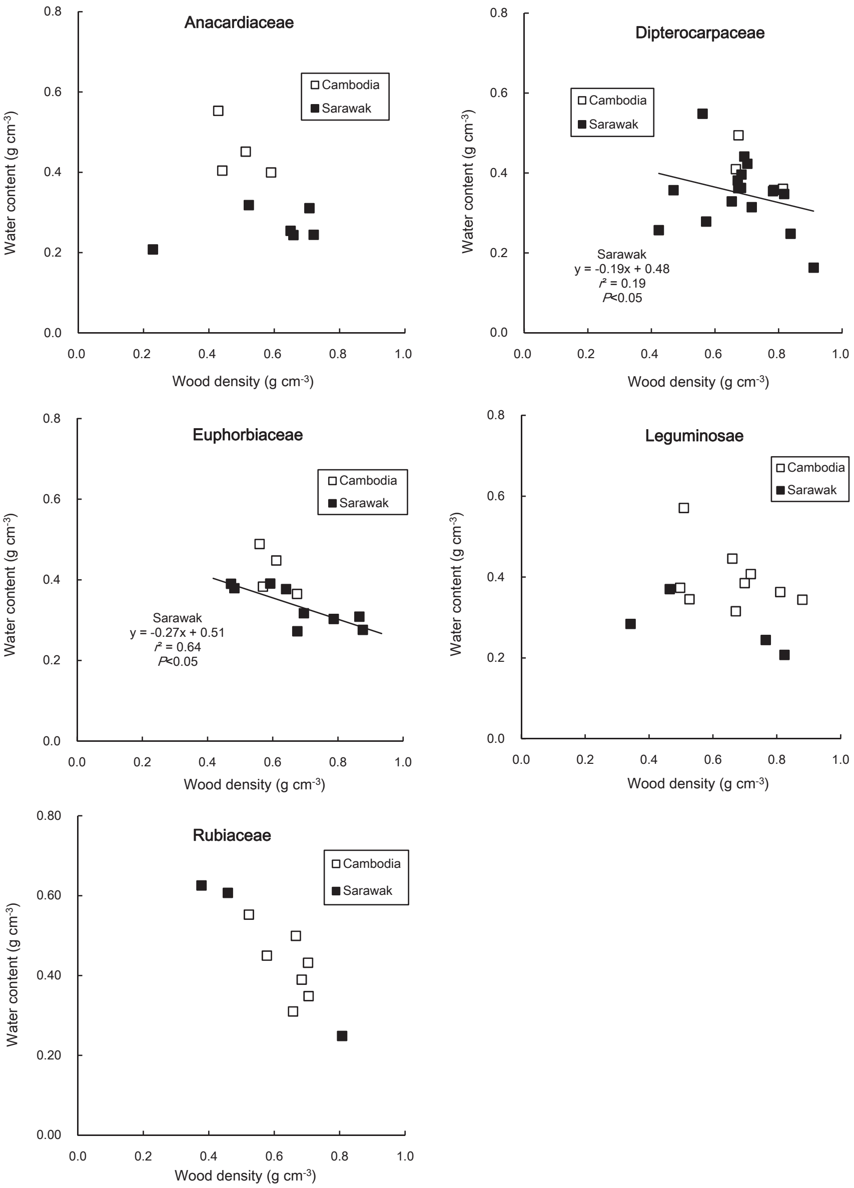

Fig. 3 Relationship between wood density and water content in major families in Cambodia and Sarawak.

considered to be used for flushing new leaves and refilling vessels in sapwood before the first rain during the dry season in dry deciduous forest trees, because the wood water content in stems in several deciduous trees was observed to significantly decrease in the dry season compared with that in the wet season (Sobrado 1993; Borchert 1994; Holbrook et al. 1995).

Relationship between wood density and water content

Cambodia and Sarawak forest trees also differed in the relationship between wood density and water content (Fig. 2). A negative correlation between wood density and water content was found in dry dipterocarp forest in Cambodia. This trend indicated that trees with lower wood density tended to contain a large amount of stored water in their stems. Trees with low wood density usually consisted of many parenchyma and lumen fractions, and thus those components could contain a large amount of water (Barajas-Morales 1985; Holbrook et al. 1995). In contrast, the correlation in Sarawak trees was less significant, and even trees with low wood density showed low water content (Fig. 2). Consistent with the findings of our study, Suzuki (1999) and Osunkoya (2007) also found little correlation between wood density and water content in various tree species in lowland dipterocarp forests in West Kalimantan and Brunei, respectively. On the other hand, several tree groups such as Dipterocarpaceae and Euphorbiaceae in Sarawak showed a significant negative correlation between wood density and water content (Fig. 3). Suzuki (1999) and Osunkoya (2007) also found similar negative relations in Dipterocarpaceae and Euphorbiaceae, respectively. Thus, the relation between wood density and water content may depend on the phylogenetic group.

Conclusions

Although dry dipterocarp (Cambodia) and lowland dipterocarp (Sarawak) forest trees did not differ in average wood density, they did significantly differ in wood water content. The higher water content observed in dry dipterocarp forest trees may indicate the importance of stem water storage under the drier environment. Our results also indicate that the relationship between wood density and water content may depend on the phylogenetic group.

Acknowledgements

The authors thank the Sarawak Forestry Cooperation, the Sarawak Forest Department, Forest-Wildlife Research and Development Institute and Drs. M. Sano, A. Shimizu, T. Sato, and E. Itoh for their kind support of this study.

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