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SHORT COMMUNICATION

Relationships of wood density and wood chemical traits between stems and coarse roots across 53 Bornean tropical tree species

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Abstract: Wood density and wood chemical traits are strong predictors of tree performance, carbon stock, and wood decomposition, which play important roles in ecosystem processes and carbon and nutrient cycling in forests. However, it remains unknown how root wood traits are related to stem wood traits. We examined the relationships of wood density and wood chemical traits (lignin and nitrogen concentrations, carbon-to-nitrogen ratio) between the stems and coarse roots of 90 individuals representing 53 tropical tree species in Malaysian Borneo. We developed regression equations of each wood trait using the standardized major axis method. Each root wood trait was highly correlated with the corresponding stem wood trait, and most regression equations fitted well ($R^2 > 0.5$). The lignin concentration of roots was significantly greater than that of stems. We conclude that root wood traits can be estimated from the corresponding stem wood traits in South-East Asian tropical trees. Further analysis of coarse root decomposability will provide more accurate estimates of carbon and nutrient fluxes in tropical forest ecosystems.

Key Words: carbon stock, C/N, decomposition, functional trait, lignin

Wood plays an important role in the performance and life-history strategies of trees, conferring mechanical stability, defence against pathogen and herbivore attacks, tree architecture and hydraulics (Falster 2006, Hoeber *et al.* 2014, Iida *et al.* 2012, Poorter *et al.* 2010). Recent studies have also found that wood density and wood chemical traits such as lignin and nitrogen (N) concentrations and carbon-to-nitrogen ratio (C/N) are good predictors of above-ground biomass and wood decomposition rates (Chave *et al.* 2015, Freschet *et al.* 2012, van Geffen *et al.* 2010, Weedon *et al.* 2009). Given the fact that a large amount of biomass is stocked as wood in forests, quantifying wood-trait variation among species will contribute to a better understanding of C stock and nutrient cycling in forest ecosystems.

Wood density and wood chemical traits have often been measured in stems and branches in the tropics (Poorter *et al.* 2010, van Geffen *et al.* 2010). Because roots comprise up to *c.* 20% of the total biomass in tropical forests (Niiyama *et al.* 2010, Poorter *et al.* 2012), differences in wood density and wood chemical traits between above- and below-ground parts could affect C pool and wood decomposition rate, and consequently, C fluxes and nutrient cycling. However, few studies have focused on the relationship between stem/branch and root wood (but see Fortunel *et al.* 2012, 2014; Freschet *et al.* 2010, Schuldt *et al.* 2013). Wood density also depends on adult stature (Poorter *et al.* 2010), suggesting that the relationships of wood density and wood chemical traits between stems and roots might vary with adult stature. However, sampling coarse roots is challenging. If researchers could estimate root wood traits by studying stems, sampling effort and damage to trees could be reduced, which would be a major technical advance in plant ecology. Here, we examined the relationships of wood density and wood chemical traits between the stems and roots of 53 coexisting Bornean rainforest tree species. We focused on stems and coarse woody roots because of their large biomass (Niiyama *et al.* 2010). Specifically, we investigated the following hypotheses: (1) Root wood traits can be estimated from stem wood traits, (2) The stem-root relationships differ with adult stature.

This study was carried out in a mixed dipterocarp lowland forest at Lambir Hills National Park, Sarawak, Malaysia (4°12′N, 114°02′E). We selected 90 individuals from 53 species representing 12 families and 21 genera,

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Table 1. Wood density and wood chemical traits of stems and coarse roots for each life form and all species measured on 53 Bornean tropical tree species (mean ± SE). Different letters indicate significant differences between stems and coarse roots for all species ($P < 0.05$).

Life form	Sp	N	Dbh (cm)	Wood density (g cm^{-3})	Lignin (%)	Nitrogen (g kg^{-1})	C/N
Stem							
Tall tree	19	41	44.8 ± 2.7	0.67 ± 0.04	31.0 ± 1.07	1.9 ± 0.03	263 ± 10.3
Medium–tall tree	24	32	32.8 ± 1.7	0.74 ± 0.02	31.2 ± 0.86	2.1 ± 0.16	249 ± 16.2
Small tree	10	17	22.4 ± 2.8	0.70 ± 0.04	29.9 ± 1.99	2.3 ± 0.14	212 ± 11.9
All species	53	90		0.71 ± 0.02[a]	30.9 ± 0.65[a]	2.1 ± 0.08[a]	247 ± 8.7[a]
Root							
Tall tree				0.70 ± 0.03	34.0 ± 0.89	2.1 ± 0.03	242 ± 10.6
Medium–tall tree				0.74 ± 0.02	32.2 ± 0.91	2.5 ± 0.23	223 ± 15.7
Small tree				0.70 ± 0.03	32.1 ± 1.84	2.5 ± 0.09	193 ± 6.9
All species				0.72 ± 0.02[a]	32.8 ± 0.62[b]	2.4 ± 0.11[a]	224 ± 8.4[a]

including abundant and common taxa at the study site. Tree species were classified into three life forms according to the adult stature: tall trees, > 30 m in height; medium–tall trees, 15–30 m; and small trees, 5–15 m (Jawa & Chai 2007; Table 1). In September 2013, we took 5–15 cm wood cores from the stems and roots of each individual using an increment borer (5.15 mm radius). These were sampled from trunks at heights of 0.5–1.0 m, and from coarse roots within a radius of 1.5 m from trunks after excavation of the base.

We measured four wood traits of stems and coarse roots: wood density, N concentration, lignin concentration and C/N. Wood density (g cm^{-3}) was calculated as dry mass to fresh volume. Carbon and N concentrations (g kg^{-1}) were measured using a CN analyser (Macro corder, JM1000CN, Yanaco, Japan). Lignin concentration (%) was determined as acid-insoluble lignin by the common Klason lignin procedure. We measured all of the wood traits in each tree, and averaged them for each species.

To examine relationships of wood density and wood chemical traits between stems and coarse roots considering taxonomic lineage, we performed correlations including phylogenetically independent contrasts (PICs). We constructed a phylogenetic tree for the 53 species using PhyloMatic v.3 utility (Webb & Donoghue 2005) based on the phylogenetic hypothesis of Davies *et al.* (2004), with polytomies applied within most families and genera. For this analysis, branch lengths were scaled to one. Each wood trait was also compared between stems and coarse roots using Welch's *t*-tests. We developed regression equations for each wood trait by the standardized major axis (SMA) method. To explore differences in the stem-root relationships among life forms, we used tests for common slope and elevation (intercept) among SMAs. When no significant difference was detected in the SMA, a common equation was regressed using pooled data for all species irrespective of life forms. All of the analyses were conducted using R 3.0.2 (packages ape and smatr).

Correlations with PICs showed that stems and coarse roots were strongly correlated for each wood trait (Figure 1). Most regression equations fitted well, and on average, explained 56% of the variation in wood traits (range = 0.18–0.81). The lignin concentration in coarse roots was significantly greater than that in stems ($P < 0.05$; Table 1). SMA regression analyses detected significantly different slopes in the regression between N concentration of stems and roots among life forms; small trees had a lower slope than tall and medium–tall trees (Figure 1).

We found that wood density and wood chemical traits of roots mirrored those of stems; thus they can be estimated from stem wood traits in Bornean tropical trees. Similar relationships between stem and root wood traits have been reported in Neotropical trees (Fortunel *et al.* 2012) and subarctic plants (Freschet *et al.* 2010). Our results will aid a greater understanding of underground C pool, C fluxes and nutrient cycling. The difference between stems and coarse roots was found only in lignin concentration. Because lignin is known to inhibit microbe and insect attacks (Bhuiyan *et al.* 2009, Wainhouse *et al.* 1990) and roots can be infested by various herbivores (Blossey & Hunt-Joshi 2003), a higher lignin concentration in roots might be effective for defence against root feeders. Higher concentration of lignin in coarse roots than in stems also indicates that wood decomposition rates of coarse roots are slower than those of stems in Bornean tropical rain forests. This hypothesis has been rarely examined, but is supported by a study of two species in a boreal forest (Freschet *et al.* 2012). Since substantial stocks of woody debris are provided underground after trees die, the differences in wood chemical traits and wood decomposability between stems and coarse roots might affect C and nutrient cycling in a forest. The different stem–root relationship in N concentration among life forms might reflect interspecific variation in N allocation between above- and belowground parts (Millard & Grelet 2010). To ensure generality and elucidate mechanisms, N allocation between stems and coarse roots in adult trees in situ should be examined. There is an increasing need for accurately estimating C stocks and fluxes in a forest ecosystem due to global climate change. We thus must

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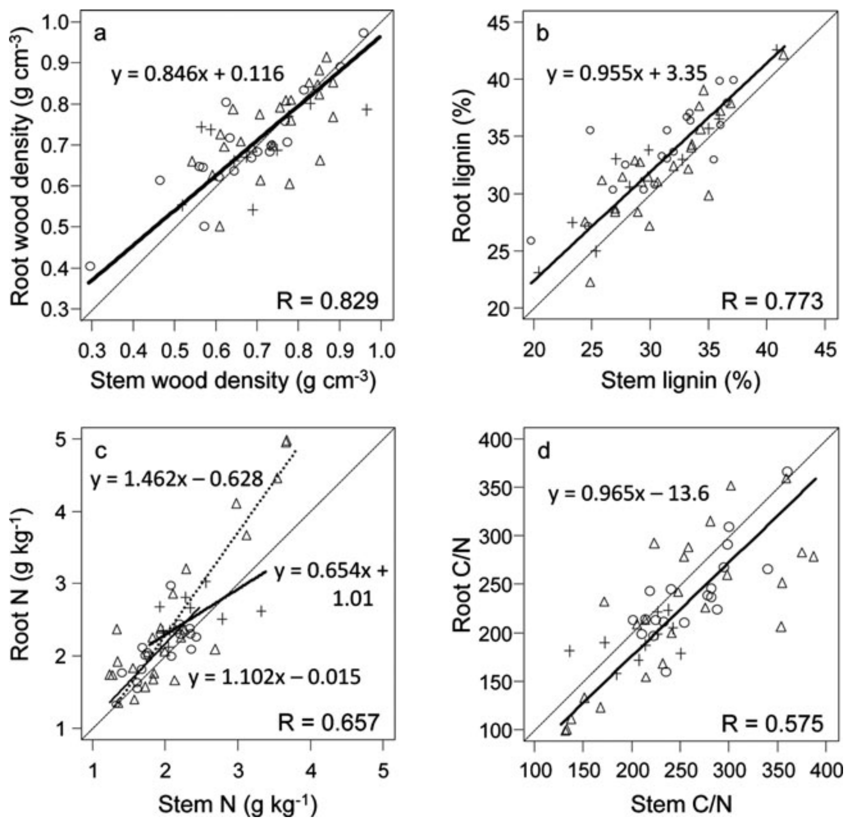

Figure 1. Relationships between stems and coarse roots for 53 Bornean tropical tree species, with Pearson correlation coefficients for PICs (R; $P < 0.05$ using Bonferroni correction) and equations in SMA regression analyses. Wood density (a); lignin concentration (b); N concentration (c); and C/N (d). Circles, triangles, and crosses indicate species of tall, medium-tall, and small trees, respectively. Thin dashed lines are 1:1 lines. Regression lines by SMA are also shown in thick lines for all species data (a, b, d). For (c), solid, dashed, and thick lines are SMA regression lines for tall, medium-tall, and small trees, respectively.

quantify wood density and wood chemical traits of both stems and coarse roots in various biomes.

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