Intra- and interspecific variation in wood density and fine-scale spatial distribution of stand-level wood density in a northern Thai tropical montane forest

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(*Accepted 20 April 2009*)

Abstract: Tropical tree wood density is often related to other species-specific functional traits, e.g. size, growth rate and mortality. We would therefore expect significant associations within tropical forests between the spatial distributions of stand-level wood density and micro-environments when interspecific variation in wood density is larger than intraspecific variation and when habitat-based species assembly is important in the forest. In this study, we used wood cores collected from 515 trees of 72 species in a 15-ha plot in northern Thailand to analyse intra- and interspecific variation in wood density and the spatial association of stand-level wood density. Intraspecific variation was lower than interspecific variation (20% vs. 80% of the total variation), indicating that species-specific differences in wood density, rather than phenotypic plasticity, are the major source of variation in wood density at the study site. Wood density of individual species was significantly negatively related to maximum diameter, growth rate of sapling diameter and mortality of saplings. Stand-level mean wood density was significantly negatively related to elevation, slope convexity, sapling growth rate and sapling mortality, and positively related to slope inclination. East-facing slopes had significantly lower stand-level mean wood densities than west-facing slopes. We hypothesized that ridges and east-facing slopes in the study forest experience strong and frequent wind disturbance, and that this severe impact may lead to faster stand turnover, creating conditions that favour fast-growing species with low wood density.

Key Words: Doi Inthanon, reduced major axis regression, spatial association, Thailand, tropical montane forest, wood specific gravity

INTRODUCTION

Wood density (specific gravity) is often related to other ecological traits such as mortality (Muller-Landau 2004, Osunkoya *et al.* 2007), growth rate (King *et al.* 2005, Suzuki 1999, Wright *et al.* 2003), mechanical properties (van Gelder *et al.* 2006), hydraulic properties (Hacke & Sperry 2001, Hacke *et al.* 2001) and shade tolerance (van Gelder *et al.* 2006). Because of these correlations, we may expect differences in the wood density of species to at least partially reflect differences in function (Swenson & Enquist 2007, Wright *et al.* 2007). Since spatial distributions of tree species in tropical forests are often associated with microhabitat within a local area (Davies *et al.* 2005, Gunatilleke *et al.* 2006, Harms *et al.* 2001, Itoh *et al.* 2003, John *et al.* 2007), we would expect that the spatial distribution of species is caused at least

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partly by functional differences among species (Kraft *et al.* 2008). We therefore postulated significant associations between spatial distributions of stand-level wood density and microhabitat.

Both positive and negative data exist for a spatial association between wood density and microhabitat. In a Costa Rican tropical montane forest, Lawton (1984) found that the stand-level wood density was higher on ridge crests than slopes and ravines, probably due to species-specific differences in mechanical tolerance toward wind. Kraft *et al.* (2008) reported that stand-level wood density was higher on ridges than valleys within a 25-ha lowland rain forest in Ecuador. However, Paoli *et al.* (2008) found only small differences in stand-level mean wood densities among forests on alluvial, sedimentary and granite soils within a 340-ha area in Gunung Palung, West Kalimantan, Indonesia.

We should take into account the phenotypic plasticity of wood density because wood density is known to vary not only among species but also within species with genetic differentiation and growing conditions (Koubaa *et al.* 2001). If intraspecific variation is substantially large within a local population, the observed relationships between wood density and microhabitats are possibly due to the difference in micro-environments rather than the species-specific difference in wood density. However, few studies have examined intraspecific variation in wood density of tropical tree populations (Osunkoya *et al.* 2007).

In this study, we hypothesized that wood density reflects species-specific difference in function and difference in wood density would cause spatial associations between tree species and topographic habitat in a northern Thai tropical montane forest. We measured the wood density of 515 trees of 72 common species within a 15-ha plot, and analysed intra- and interspecific variation and spatial distributions of stand-level wood densities. Our specific objectives were to evaluate the relative importance of intra- and interspecific variation in wood density; analyse the relationships between wood density and other ecological traits, i.e. maximum size, sapling mortality and sapling growth by species; and analyse fine-scale spatial distribution of stand-level wood density and its relationship to topography.

METHODS

Study site and permanent plot

The study was conducted in Doi Inthanon National Park, northern Thailand (18°24′–18°40′ N, 98°24′–98°42′ E). The park covers an area of 482 km², and its elevation ranges from 400 to 2565 m asl. Mean annual rainfall and mean monthly minimum and maximum temperatures at the Royal Project Doi Inthanon Station (1300 m asl;

1993–2006) were 1940 mm, 16.4 °C and 26.3 °C, respectively. A distinct seasonality occurs in rainfall; the dry season is from December to April and the rainy season starts in May and ends in November. The vegetation of Doi Inthanon National Park is divided into three zones along elevation gradients: the lowland (400–850 m asl), transitional (850–1400 m asl) and montane (1400–2500 m asl) zones (Teejuntuk *et al.* 2002). The montane zone is further divided into lower and upper montane forests at approximately 1800 m asl (Santisuk 1988). Tree species diversity increases with elevation up to around 1800 m, and then decreases toward the summit (Teejuntuk *et al.* 2002).

A 15-ha permanent plot was established within the lower montane forest zone, which had the most diverse vegetation at the site (18°31′24″N, 98°29′42″E, *c.* 1700 m asl). Bedrock within the plot comprises post-Silurian and post-Permian granite and pre-Cambrian gneiss (Pendleton 1962). Soils in the plot are coarse, sandy and well drained (Kanzaki *et al.* 2004). The relative elevations at 10×10-m grid points in the plot were measured using a surveying instrument with a compass and a level (LS-25; Ushikata Co. Ltd., Tokyo, Japan). All living trees $\geq$ 1 cm in diameter at breast height (dbh; 140 cm above the ground) were measured, tagged, mapped and identified to species. The first tree census was completed in March 2000 and the second in March 2003. In terms of basal area, Fagaceae and Lauraceae were the dominant families. The most abundant species was *Mastixia euonymoides* (Cornaceae) followed by *Quercus eumorpha* (Fagaceae), *Manglietia garrettii* (Magnoliaceae), *Calophyllum polyanthum* (Guttiferae), *Quercus brevicalyx* (Fagaceae) and *Cryptocarya densiflora* (Lauraceae). Further details of the plot are given elsewhere (Hara *et al.* 2002, Kanzaki *et al.* 2004, Noguchi *et al.* 2007, Sri-ngernyuang *et al.* 2003).

Wood density measurement

Wood densities were measured for all common species that had more than five individuals in the 15-ha plot (72 species, 54 genera, 33 families; Appendix 1). For each species, 4–26 sample trees (mean = 7.2) were selected from a variety of topographies within the plot. We selected sample trees of various sizes in each species, but all were > 10 cm dbh. The dbh range of sampled trees was 10–158 cm, varying with the maximum size of each species. A wood core was extracted from each sample tree between 1 and 1.3 m above the ground on the uphill side of the trunk using an increment borer with a 5.15 mm core diameter (Mattson, Mora, Sweden). The average length of the wood core was 90 mm for smaller trees (dbh < 30 cm) and 150 mm for larger trees (dbh > 30 cm). The diameters at both ends of each core and its length were measured

immediately with digital callipers. The green volume was calculated by multiplying the length by the mean cross-sectional area of the two ends. All wood samples were oven-dried at 85 °C to constant mass (usually 5–7 d), and then weighed to the nearest 0.001 g. Wood density was calculated as dry weight divided by green volume. For more details of wood density measurement, see Chave *et al.* (2006).

Analysis of intra- and interspecific variation

To determine the degree of phenotypic variation in wood density within a species, we used analysis of variance (ANOVA) to partition total variance in wood density (across all samples, $n = 515$) into family, genus and species levels. When intraspecific variation is small compared with interspecific variation, a larger proportion of the total variance would be attributable to species.

Demographic properties of species

To analyse correlations between wood density and demographic properties of species, we calculated maximum sizes, mortality rates and dbh growth rates for the study species. Maximum size was the maximum diameter of each species that we found in the plot. Relative dbh growth rate (RGR; y^{-1}) was calculated for each individual as $(lnD_1 - lnD_0)/\Delta T$, where D_0 and D_1 are the dbh values at the first and second census, respectively, and ΔT is the time interval between the two censuses (interval range was 2.9–6.1 y). Subsequently, RGRs were averaged for each species. Annual mortality (λ), or specifically, the exponential mortality coefficient (Sheil *et al.* 1995), is expressed by

$$\lambda = -\frac{1}{N}\frac{dN}{dt}, \tag{1}$$

where N is the number of trees and t is time in y. We made estimates for each species using a maximum-likelihood method (Kubo *et al.* 2000). Growth and mortality rates were calculated only for saplings ($1 \leq$ dbh ≤ 5 cm) because these parameters were size-dependent and we could not get reliable values for larger trees of many species due to small sample sizes. We omitted the growth and mortality rates of two species with < 30 saplings in the plot.

Relationships between wood density and each demographic trait (i.e. maximum diameter, RGR and mortality rate) were analysed by model II regression analysis (which is known as reduced major axis analysis (RMA)) since both wood density and demographic traits include estimation errors. Confidence intervals for regression slopes were calculated with standard linear regression approximations (Sokal & Rohlf 1995). The RGR and mortality rate were log_{10}-transformed before analysis.

Spatial distribution of wood density

To check local spatial distribution of stand-level wood density, we divided the plot into 375 20×20-m quadrats and calculated two types of mean wood density for each quadrat, i.e. the stem-based mean (STM) and the basal area-based mean (BAM). Stem-based mean and BAM were calculated with the following equations:

$$STM = \frac{\sum\limits_{i=1}^{n} WD_i}{n} \tag{2}$$

$$BAM = \frac{\sum\limits_{i=1}^{n} BA_i WD_i}{\sum\limits_{i=1}^{n} BA_i}, \tag{3}$$

where n is the number of individuals in a focal quadrat and WD_i and BA_i are wood density and basal area of the ith individual, respectively. We used genus mean values of wood density when species-level wood density was not available for the ith individual ($n = 4013$). Genus-level averages are known to relate well to species-level wood densities and can be used when values for species are unavailable (Chave *et al.* 2006, Slik 2006); we also found that 71% of the total variance in wood density was attributable to genus-level variance in our wood samples, as mentioned below. Individuals were excluded from the analysis when both species- and genus-level values were unavailable because we were unable to obtain reliable wood-density data; these trees were 17.9% in number and 1.7% in basal area of all trees in the plot.

Relationships between STM or BAM and topography, growth rates and mortalities for the 20×20-m quadrats were analysed by RMA. Mean dbh, RGR and mortality were calculated for each quadrat using saplings (1 cm $\leq$ dbh ≤ 5 cm) of all species in a focal quadrat. Four topographic variables (i.e. relative elevation, slope inclination, slope aspect and index of convexity (IC)) were calculated for each quadrat using the method of Yamakura *et al.* (1995). Elevation, inclination and aspect were obtained from a three-dimensional regressed plane of each quadrat, which was determined by the relative elevations at four corner points of a focal quadrat. Index of convexity was defined as the difference between the mean elevation of the four corner points and the elevation measured at the centre of the quadrat. Positive and negative IC values indicate convex and concave land surface features, respectively. Index of convexity is an index of land surface features at a very local scale, while elevation indicates larger-scale topography such as main

Table 1. Proportions of wood density variance attributable to different taxonomic levels ($n = 515$ trees in Doi Inthanon National Park, Thailand). Variance proportions were derived from ANOVA. *F*-ratios and significance levels (*** $P < 0.001$) are given.

Taxonomic level	df	F	Fraction of variance explained
Family	32	10.9***	0.421
Genus	53	21.7***	0.714
Species	71	25.8***	0.806

ridges. Slope aspect was converted to bearing from the east ($0°–180°$) because wind direction was prevalently westerly at the study site (Noguchi *et al.* 2007). Therefore, western and eastern slopes corresponded approximately to windward and leeward slopes, respectively. This was partially confirmed by field observation in that the majority of recent large tree falls were directed eastward (Sungpalee, pers. obs.). Relative dbh growth rate and mortality rate were $\log_{10}$-transformed before analysis. All the statistical analyses were performed with R 2.8.1 software (The R Development Core Team, http://www.r-project.org).

RESULTS

Intra- and interspecific variation in wood density

Of wood density total variance ($n = 515$), 80%, 71% and 42% were attributable to interspecific, intergeneric and interfamilial variation, respectively (Table 1). Thus, the intraspecific variance component is relatively small (20% of the total) compared with interspecific variation (80%). The small intraspecific variation was also detected by low within-species coefficients of variation (CV), which ranged from 2.6% to 23.4%, with a mean of 8.1% (Appendix 2).

Figure 1 shows the distribution of mean wood density by species. Mean wood density across species was 0.549 ± 0.043 (SD) g cm^{-3}, ranging from 0.333 g cm^{-3} (*Macaranga denticulata*, Euphorbiaceae) to 0.731 g cm^{-3} (*Quercus brevicalyx*, Fagaceae) (Appendix 2). The distribution was not significantly different from a normal distribution tested by the one-sample Kolmogorov–Smirnov test ($P = 0.531$) and the Shapiro–Wilk normality test ($P = 0.325$).

Species wood densities were significantly negatively correlated with maximum diameter, RGR of saplings and mortality of saplings. The slopes of RMA regression lines were -0.0032 (95% CI: -0.0040 to -0.0024), -0.630 (95% CI: -0.777 to -0.483) and -0.317 (95% CI: -0.392 to -0.242) for maximum diameter, RGR and mortality, respectively. Species with larger maximum
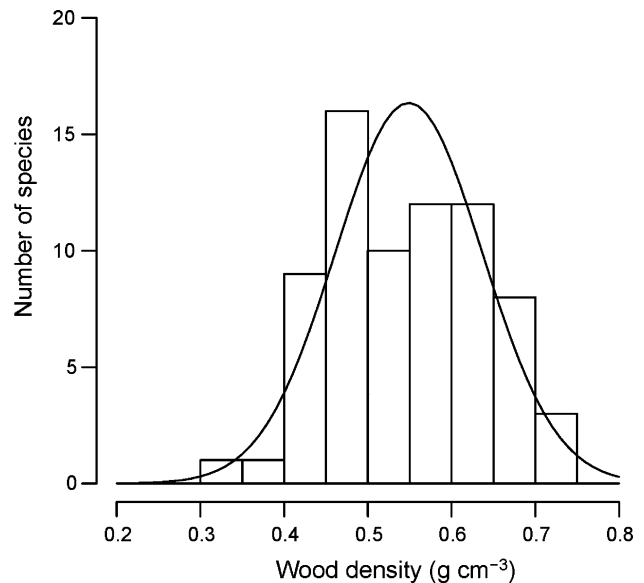
Figure 1. Frequency distribution of wood densities for 72 common tree species in Doi Inthanon National Park, northern Thailand. The solid line is the fitted normal probability distribution.

diameters, rapid sapling growths and higher mortality rates tended to have lower wood density.

Spatial distribution of wood density

Stand-level wood densities based on stem number (STM) and basal areas (BAM) varied considerably within the plot. The mean STM was 0.555 ± 0.021 (SD) g cm^{-3} (range = 0.47–0.60 g cm^{-3}; CV = 3.8%) and BAM was 0.559 ± 0.037 g cm^{-3} (range = 0.46–0.66 g cm^{-3}; CV = 6.5%). Based on the ranges, the within-plot differences increased 1.3- and 1.4-fold for STM and BAM, respectively.

The spatial distributions of STM and BAM are illustrated in Figure 2, which also shows the distribution of stand-level mean RGR of saplings (Figure 2c) and the mortality rate of saplings (Figure 2d). Stem-based mean was significantly negatively correlated with elevation, convexity, RGR and mortality, and positively correlated with inclination and aspect (Figure 3). Basal area-based mean was similarly related to topography and demographic traits, except that BAM was related positively to convexity (STM was related negatively to convexity) (Table 2).

DISCUSSION

Intraspecific variation in wood density

Intraspecific variation was smaller (20% of the total wood density variation in sample trees) than interspecific

(a) STM

(b) BAM

(c) RGR of saplings

(d) Mortality rate of saplings

100 m

N
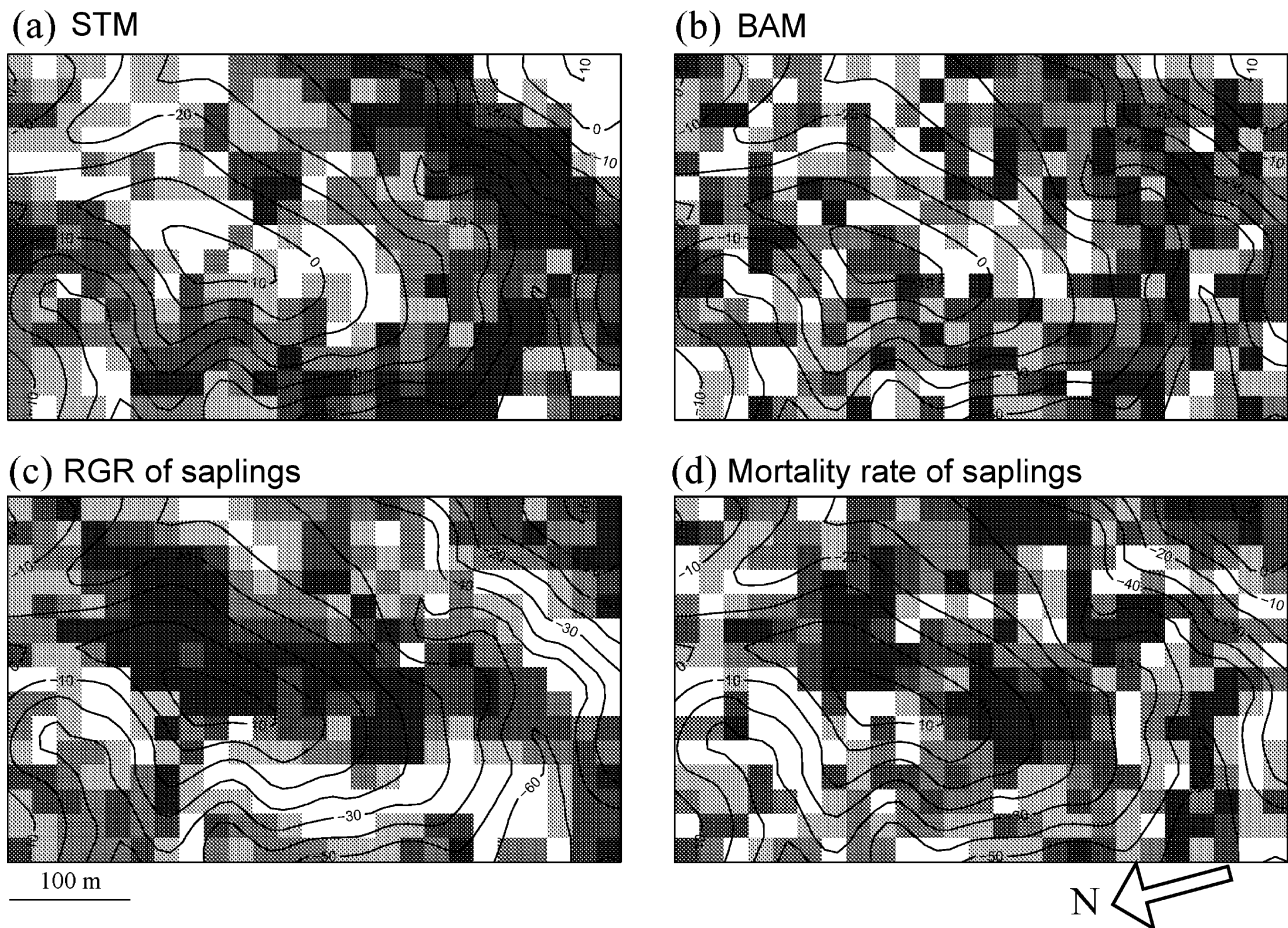
Figure 2. Spatial distribution of stem-based mean wood density (STM) (a), basal area-based mean wood density (BAM) (b), mean relative growth rate (RGR) of saplings ($1 \leq$ dbh ≤ 5 cm) (c) and mean mortality rate of saplings (d) in a 15-ha plot in Doi Inthanon National Park, northern Thailand. Values were calculated for 20×20-m quadrats and divided into four quintile classes. Darker shading indicates higher values. Topographic contours of 10-m intervals are also shown.

Table 2. Slopes of reduced major axis regressions between basal area-based mean wood density (BAM) and demographic traits of saplings ($1 \leq$ dbh ≤ 5 cm) and topography within 20×20-m quadrats in a 15-ha plot at Doi Inthanon National Park, northern Thailand. RGR: relative growth rate of diameter; λ: annual mortality. Topographic variables were calculated from a regressed plane for each square; positive and negative values of the index of convexity indicate convexity and concavity, respectively, of land surface at a very local scale. Ninety-five per cent confidence intervals are also given.

Variables	Slope	95% CI
Demographic traits		
$\log_{10}$RGR	−0.159	−0.1749 − −0.1430
$\log_{10}\lambda$	−0.121	−0.1339 − −0.1092
Topography		
Relative elevation (m)	−0.0019	−0.0021 − −0.0017
Slope aspect (°)	0.0008	0.0007 − 0.0008
Slope inclination (°)	0.0041	0.0036 − 0.0047
Index of convexity (m)	0.0354	0.0318 − 0.0390

variation, even though we collected wood samples from variously sized trees growing under diverse topographic conditions. For comparison, we calculated the CVs of

intraspecific variation in wood density for trees in a Brunei lowland tropical rain forest (data from Table 1 in Osunkoya *et al.* 2007). They measured the wood density of 209 trees in 27 species (4–22 trees per species; mean = 7.7 trees per species) in a 1-ha plot. The mean CV of the 27 species was 13.4% (range: 6.4–25.0%), which was slightly larger than that of this study (mean = 8.1%; range: 2.6–23.4%). The small intraspecific variation in the current study indicates that species-specific differences (not intraspecific variation and phenotypic plasticity) are a major determinant of the relationships between wood density and species traits, and between stand-level mean wood density and topography, at least in our study forest.

Interspecific variation and relationships to other traits

Mean wood density (0.55 g cm^{-3}) across the 72 species studied was comparable to, or slightly lower than, within-site species means of wood densities reported for Asian
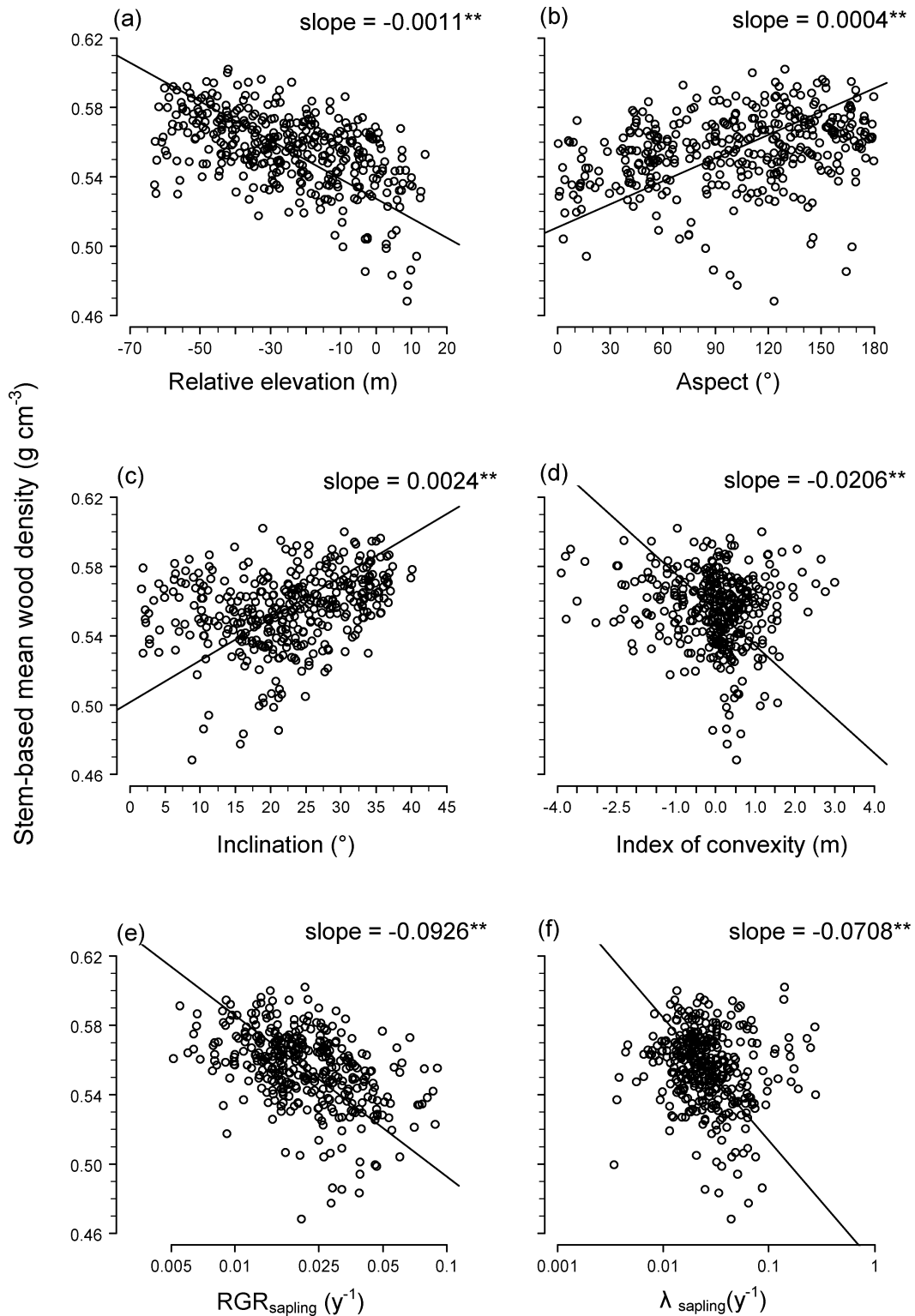
Figure 3. Relationship between stem-based mean wood density (STM) and topography and demographic traits in 20×20-m quadrats within a 15-ha plot ($n = 372$): relative elevation (a), slope aspect (b), slope inclination (c), index of convexity (d), relative growth rate (RGR) of saplings ($1\,cm \le dbh \le 5\,cm$) (e) and mortality rate (λ) of saplings (f). Solid lines are regression lines generated via a reduced major axis regression. Slopes of the regression lines are also shown; ** indicates slope is significantly negative or positive at $P < 0.01$.

lowland tropical rain forests, e.g. 0.56 g cm^{-3} in West Kalimantan (Suzuki 1999) and 0.59 g cm^{-3} in Brunei (Osunkoya *et al.* 2007); in the Neotropics, the mean wood density was 0.54 g cm^{-3} in Panama, 0.56 g cm^{-3} in Costa Rica, 0.56 g cm^{-3} in Peru and 0.70 g cm^{-3} in Brazil (Muller-Landau 2004). The range of wood density found in this study (0.398 g cm^{-3}) is smaller than the within-site ranges reported for these other rain forests (0.40–0.66 g cm^{-3}).

The significant negative relationships between wood density and species mortalities or growth rates are generally consistent with previous studies in lowland rain forests, such as those in Panama (Muller-Landau 2004), the Amazon (Chao *et al.* 2008), Peninsular Malaysia (King *et al.* 2005), West Kalimantan (Suzuki 1999) and Brunei (Osunkoya *et al.* 2007). These relationships are often considered a reflection of trade-offs between growth and mortality via traits such as mechanical strength, shade-, pathogen- and drought-tolerance (Wright *et al.* 2007).

Large-statured species with light wood

We found a significant negative correlation between wood density and maximum diameter of the species studied. This was at least partially due to unique features of the tree flora and structure in the study forest, which contained a group of huge canopy species with relatively low wood density, such as *Mastixia euonymoides* (wood density $= 0.49$ g cm^{-3}; maximum dbh $= 176$ cm) and *Manglietia garrettii* (wood density $= 0.44$ g cm^{-3}, maximum dbh $= 157$ cm) (Kanzaki *et al.* 2004). *Mastixia euonymoides* and *M. garrettii* were the first and second largest species, respectively, in the study plot (in terms of maximum dbh). *Mastixia euonymoides* and *M. garrettii* were ranked first and fourth, respectively, in terms of basal area dominance. Chave *et al.* (2004) also reported that wood density was lower in large trees in a Panamanian forest, probably due to the high dominance of large species with light wood, such as *Ceiba pentandra* (Bombacaceae; wood density $= 0.31$ g cm^{-3}). The reason why species with light wood are dominant in the upper canopy of these forests has yet to be resolved.

Spatial variation in stand-level wood density

The range of stand-level mean wood densities within the 15-ha plot (0.47–0.60 g cm^{-3} and 0.46–0.66 g cm^{-3} for STM and BAM, respectively) was smaller than that among species (0.333–0.731 g cm^{-3}). This is, however, not surprising since stand-level averages across individuals naturally constrain the range. To evaluate the degree of stand-level variation, we need to compare these values with those of other studies.

To date, we have found only one study with which we were able to compare our data on spatial variation in stand-level wood density. Kraft *et al.* (2008) calculated STMs of 20×20-m quadrats within a 25-ha plot in an Ecuadorian Amazonian lowland rain forest; although they did not measure wood density of the trees in the plot, they used species wood densities obtained from the literature. The range of species wood densities was larger in the Amazonian forest (*c.* 0.1–1.0 g cm^{-3} for 256 species) than in the plot we studied in Thailand (0.33–0.73 g cm^{-3} for 72 species), but the STM ranges were very similar for both forests: 0.47–0.60 g cm^{-3} and *c.* 0.52–0.64 g cm^{-3} for the Thai and the Amazonian forests, respectively. The combination of relatively large STM range and small species-level range in the forest we studied was not expected; a possible explanation is that spatial aggregation among species with similar wood densities may be stronger at our site than in the Amazonian forest.

Relationship between wood density and topography

Stand-level wood density was lower at higher elevations and on eastern slopes than at other locations within the study plot (Figures 2, 3; Table 2). This is the reverse of the density/topographic relationships within a Costa Rican montane forest and within an Ecuadorian lowland rain forest. Stand-level wood density was higher on ridges in these New World forests (Kraft *et al.* 2008, Lawton 1984).

A possible explanation for the discrepancy between the present study and earlier works may be found in differing wind disturbance effects. At our site, the ridges may be impacted more strongly and more frequently by gale- or storm-force winds than the lower slopes. The severe disturbance may lead to a more rapid turnover of trees, creating conditions that favour fast-growing species, which typically have low wood density. In the forests studied by Lawton (1984), disturbance by wind may be less severe because canopy trees on the ridges were much shorter (5–10 m) than those in our plot (> 30 m), and these short individuals were probably more tolerant of strong wind forces. Wind effects are likely to be minimal even on ridges in the Ecuadorian lowland forest, where wind is generally weak.

This explanation is consistent with our finding that on the ridges and eastern slopes we studied, mortality and growth rates of saplings were elevated (Figure 2c, d), while STM and BAM were negatively related to sapling mortality and RGR (Figure 3e, f). Saplings on the eastern slopes may suffer higher mortality because trees blown down on the ridges would fall mostly in an easterly direction (the prevailing strong winds are westerly). In April 2007, we also observed many recently fallen trees in our plot pointing eastward (Sungpalee, pers. obs.). If the intensity and frequency of disturbance relate to the spatial

distribution of stand-level wood density, we would expect lower turnover rates with lower mortality and growth rates on the ridges in the Costa Rican and Ecuadorian forests, but this was not studied by either Lawton (1984) or Kraft *et al.* (2008).

Alternatively, differences in micro-environments may be related to topography independent of disturbance but may still affect the spatial distribution of stand-level wood density. When soils are less fertile in valleys, the conditions may favour persistent shade-tolerant species, which have relatively high-density woods (Muller-Landau 2004). Trees on ridges may get more light than those in valleys, even without canopy gaps, and thus rapid growth would be advantageous on the ridges. Further studies, especially on spatial patterns of soils and light conditions in the plot and their effects on population dynamics, are needed to identify the causal processes producing the observed relationship between wood density and topography.

ACKNOWLEDGEMENTS

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Appendix 1. List of 72 common tree species studied in a 15-ha plot of a tropical lower montane forest in Doi Inthanon National Park, northern Thailand. N: number of trees (dbh ≥ 1 cm) in the plot.

Species	N
Aceraceae	
Acer laurinum Hassk.	1269
Aquifoliaceae	
Ilex longecaudata Comber var. *longecaudata*	560
Betulaceae	
Betula alnoides Buch.-Ham.	14
Boraginaceae	
Cordia cf. *cochinchinensis* Gagnep.	148
Capparaceae	
Capparis cf. *assamica* Hook.f. & Thoms.	492
Celastraceae	
Euonymus colonoides Craib	193
Cornaceae	
Mastixia euonymoides Prain	712
Daphniphyllaceae	
Daphniphyllum cf. *glaucescens* Blume ssp. *beddomei* (Craib) Huang	341
Ebenaceae	
Diospyros frutescens Blume	115
Elaeocarpaceae	
Elaeocarpus braceanus Watt ex C. B. Clarke	126
Elaeocarpus lanceifolius Roxb.	994
Elaeocarpus petiolaris (Jack) Wall. ex Kurz	89
Euphorbiaceae	
Drypetes indica (Mull. Arg.) Pax & Hoffm. var. *indica*	971
Drypetes sp.	1056
Macaranga denticulata (Blume) Muell.-Arg.	131
Mallotus khasianus Hook. f.	7404
Ostodes paniculata Blume	1661
Fagaceae	
Castanopsis acuminatissima (Blume) A. DC.	119
Castanopsis calathiformis Kurz	4374
Castanopsis purpurea Barnett	1575
Lithocarpus aggregatus Barnett ssp. *aggregatus*	518
Lithocarpus echinops Hjelmq.	561
Lithocarpus vestitus (Hickel & A. Camus) A. Camus	1402
Quercus brevicalyx A. Camus	955
Quercus eumorpha Kurz (Syn. = *Q. lenticellata* Barnett)	1507
Guttiferae	
Calophyllum polyanthum Wall.	6088
Icacinaceae	
Nothapodytes cf. *obscura* C. Y. Wu	190
Platea latifolia Blume	353
Juglandaceae	
Engelhardtia spicata Lesch. ex Blume var. *spicata*	33
Lauraceae	
Actinodaphne sp.	166
Beilschmiedia glauca Sin. C. Lee & L. F. Lau var. *glaucoides* H. W. Li	355
Cinnamomum bejolghota (Ham.) Sweet var. *bejolghota*	682
Cinnamomum cf. *soegengii* Kosterm.	248
Cryptocarya cf. *calcicola* H. W. Li	1051
Cryptocarya densiflora Blume	2027
Lindera metcalfiana Allen	1727
Litsea beusekomii Kostermans	1955
Litsea lancifolia Hook. f.	732
Litsea pedunculata (Diels) Yang & P. H. Huang	541
Litsea subcoriacea Yen C. Yang & P. H. Huang	819
Litsea yunnanensis Yen C. Yang & P. H. Huang	1273
Neolitsea zeylanica (Nees) Merr.	325
Persea sp.	447
Phoebe macrocarpa C. Y. Wu	127
Magnoliaceae	
Manglietia garretii Craib	738

Appendix 1. Continued.

Species	N
Meliaceae	
Dysoxylum sp. 2	253
Heynea trijuga Sims	2490
Toona ciliata M. Roem.	193
Moraceae	
Artocarpus cf. *lacucha* Ham.	200
Ficus hirta Vahl var. *hirta*	270
Myristicaceae	
Horsfieldia sp.	823
Myrsinaceae	
Ardisia rubro-glandulosa Fletcher	317
Rapanea yunnaensis Mez	728
Myrtaceae	
Syzygium angkae (Craib) P. Chantaranothai & J. Parnell ssp. *angkae*	3051
Syzygium tetragonum Wall.	1094
Nyssaceae	
Nyssa javanica Wangerin	298
Olacaceae	
Schoepfia fragrans Wall.	167
Oleaceae	
Chionanthus ramiflorus Roxb.	1142
Podocarpaceae	
Podocarpus neriifolius D.Don	55
Rhizophoraceae	
Carallia brachiata (Laur.) Merr.	90
Rosaceae	
Prunus phaeosticta (Hance) Maxim.	318
Prunus wallichii Steud	499
Rubiaceae	
Aidia yunnanensis (Hutch) T. Yamaz.	832
Tarenna disperma (Hook. f.) Pit. (Syn. = *Webera disperma* Hook. f.)	575
Sapotaceae	
Sarcosperma arboreum Buch.-Ham. ex C. B. Clarke	282
Saxifragaceae	
Polyosma integrifolia Blume	1351
Symplocaceae	
Symplocos henschelii (Mor.) Benth. ex C. B. Clarke var. *magnifica* (Fletcher) Noot.	141
Symplocos macrophylla Wall. ex DC. ssp. *sulcata* (Kurz) Noot. var. *sulcata*	2001
Theaceae	
Camellia oleifera Abel var. *confusa* (Craib) Sealy	1458
Camellia taliensis (W. W. Sm.) Melch.	239
Eurya nitida Korth. var. *nitida*	2062
Pyrenaria garrettiana Craib	201

Appendix 2. Wood density (mean ± SD) and ecological traits of 72 species studied in a 15-ha plot within Doi Inthanon National Park, northern Thailand. N: number of wood core samples; dbhmax: maximum diameter in the plot; RGR: mean relative growth rate of saplings (1 cm ≤ dbh ≤ 5 cm); λ: exponential mortality coefficients of saplings; NA: data not available due to small sample size ($n < 30$). Species are sorted by wood density in increasing order.

Species	N	Wood density (g cm^{-3})	dbh_{max} (cm)	RGR $(\% \text{ y}^{-1})$	λ $(\% \text{ y}^{-1})$
Macaranga denticulata	6	0.333 ± 0.032	44.9	5.25	16.19
Ostodes paniculata	8	0.397 ± 0.023	47.1	2.76	2.70
Engelhardtia spicata	5	0.409 ± 0.032	50.9	NA	NA
Ficus hirta	5	0.410 ± 0.058	60.6	1.60	4.38
Castanopsis calathiformis	11	0.419 ± 0.040	81.7	3.87	3.75
Platea latifolia	7	0.437 ± 0.096	56.8	3.24	1.42
Litsea lancifolia	5	0.438 ± 0.030	44.9	3.44	1.36
Manglietia garretii	22	0.438 ± 0.037	157.5	4.38	7.22
Litsea yunnanensis	6	0.441 ± 0.042	44.4	3.28	1.99
Sarcosperma arboretum	6	0.443 ± 0.037	73.5	2.98	1.58

Appendix 2. Continued.

Species	N	Wood density (g cm^{-3})	dbh$_{max}$ (cm)	RGR (% y^{-1})	λ (% y^{-1})
Artocarpus cf. *lacucha*	5	0.444 ± 0.023	44.4	2.90	2.24
Cinnamomum cf. *soegengii*	7	0.456 ± 0.053	95.8	3.84	1.87
Podocarpus neriifolius	5	0.469 ± 0.059	88.0	3.07	0.79
Dysoxylum sp. 2	5	0.471 ± 0.025	45.8	2.53	0.54
Ilex longecaudata	5	0.477 ± 0.038	69.4	1.55	0.86
Daphniphyllum cf. *glaucescens*	10	0.483 ± 0.035	62.3	2.47	5.67
Cordia cf. *cochinchinensis*	5	0.486 ± 0.081	71.9	2.53	1.81
Elaeocarpus lanceifolius	7	0.489 ± 0.078	59.2	1.86	3.53
Symplocos henschelii	5	0.490 ± 0.030	52.5	2.04	1.51
Mastixia euonymoides	26	0.490 ± 0.033	176.7	1.94	1.53
Symplocos macrophylla	6	0.491 ± 0.014	41.1	1.91	3.10
Toona ciliata	5	0.493 ± 0.073	69.5	1.97	4.85
Horsfieldia sp.	6	0.494 ± 0.035	73.9	1.95	1.14
Litsea beusekomii	5	0.494 ± 0.068	38.2	3.14	2.40
Elaeocarpus braceanus	5	0.497 ± 0.031	59.1	2.08	0.95
Litsea pedunculata	9	0.497 ± 0.057	76.9	3.52	2.64
Schoepfia fragrans	4	0.498 ± 0.082	31.3	2.51	1.79
Pyrenaria garrettiana	5	0.502 ± 0.025	46.8	2.53	2.61
Polyosma integrifolia	6	0.509 ± 0.027	59.5	2.40	1.96
Lindera metcalfiana	8	0.511 ± 0.054	56.5	4.48	7.44
Beilschmiedia glauca	5	0.522 ± 0.071	51.6	2.72	0.73
Diospyros frutescens	7	0.524 ± 0.041	68.8	2.25	2.50
Cinnamomum bejolghota	7	0.531 ± 0.066	58.0	3.04	2.05
Mallotus khasianus	6	0.534 ± 0.015	38.3	1.82	1.40
Euonymus colonoides	6	0.538 ± 0.020	31.5	1.43	1.20
Camellia taliensis	5	0.543 ± 0.034	36.4	2.40	3.09
Eurya nitida	7	0.547 ± 0.024	25.3	2.02	2.17
Nyssa javanica	5	0.550 ± 0.036	134.1	2.97	1.94
Ardisia rubro-glandulosa	5	0.554 ± 0.067	27.5	2.33	2.12
Nothapodytes cf. *obscura*	5	0.558 ± 0.020	47.1	0.90	4.24
Acer laurinum	6	0.559 ± 0.038	74.1	3.78	1.89
Cryptocarya densiflora	6	0.560 ± 0.030	66.2	3.22	1.96
Phoebe macrocarpa	5	0.575 ± 0.053	57.8	2.00	4.44
Litsea subcoriacea	5	0.578 ± 0.050	55.7	2.50	2.47
Heynea trijuga	5	0.583 ± 0.058	44.8	3.31	1.77
Castanopsis purpurea	11	0.590 ± 0.058	77.1	2.75	2.05
Elaeocarpus petiolaris	5	0.592 ± 0.039	63.6	1.77	4.49
Drypetes sp.	9	0.595 ± 0.045	77.7	1.28	1.59
Calophyllum polyanthum	20	0.599 ± 0.055	102.9	1.83	0.97
Castanopsis acuminatissima	4	0.609 ± 0.042	58.9	4.12	6.36
Aidia yunnanensis	7	0.615 ± 0.144	48.9	2.27	2.51
Neolitsea zeylanica	5	0.616 ± 0.043	52.2	2.62	2.94
Betula alnoides	6	0.617 ± 0.037	77.3	NA	NA
Drypetes indica	11	0.619 ± 0.037	55.4	1.75	0.99
Capparis cf. *assamica*	6	0.624 ± 0.033	46.7	1.91	0.69
Tarenna disperma	13	0.626 ± 0.031	51.1	2.15	1.63
Camellia oleifera	6	0.634 ± 0.025	33.4	1.70	1.55
Lithocarpus aggregatus	5	0.636 ± 0.045	68.0	2.52	2.75
Prunus wallichii	6	0.642 ± 0.029	48.4	3.55	2.40
Quercus eumorpha	17	0.642 ± 0.046	102.8	2.43	2.76
Lithocarpus echinops	6	0.646 ± 0.034	63.2	2.55	4.05
Chionanthus ramiflorus	7	0.651 ± 0.036	64.2	1.36	1.74
Syzygium tetragonum	5	0.660 ± 0.044	84.5	2.25	2.11
Carallia brachiata	5	0.661 ± 0.018	45.4	2.22	0.42
Actinodaphne sp.	7	0.661 ± 0.032	35.8	3.37	1.34
Persea sp.	9	0.665 ± 0.038	71.7	2.57	3.63
Cryptocarya cf. *calcicola*	5	0.666 ± 0.049	59.2	3.24	1.14
Syzygium angkae	8	0.670 ± 0.050	69.5	1.77	1.28
Lithocarpus vestitus	5	0.692 ± 0.032	68.9	3.05	2.13
Rapanea yunnaensis	6	0.701 ± 0.041	42.2	2.41	1.38
Prunus phaeosticta	5	0.723 ± 0.019	24.8	2.11	2.44
Quercus brevicalyx	11	0.731 ± 0.026	120.0	2.28	2.58