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Variation in wood density, wood water content, stem growth and mortality among twenty-seven tree species in a tropical rainforest on Borneo Island

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Abstract Interspecific variation among wood density (WD), wood water content (WWC), tree mortality and diameter at breast height (d.b.h.) increment was examined for 27 tree species (from 13 families), based on a 9-year interval data obtained from a permanent 1-ha forest plot setup for long-term studies of tree dynamics in Kuala Belong rainforest, Brunei, on Borneo Island. The species were also categorized into three adult stature groups of understorey (maximum height $\leq$15–20 m tall, $n = 14$), midcanopy (maximum height, 20–30 m tall, $n = 8$) and canopy/emergent (>maximum height, >30 m tall, $n = 5$) tree species. All measured traits varied appreciably among species. Tree WD varied between 0.3 and 0.8 g cm^{-3}, and exhibited the least coefficient of variation (14.7%). D.b.h. increment was low, averaging 1.05 (95% confidence limits: 0.57–2.13) mm year^{-1} and was attributed to predominance of understorey species in the sampled plot. Overall, annual mortality was also low, averaging 2.73% per year. The three adult stature groups differed significantly in d.b.h. increment and WWC but not in tree mortality and WD. Across species and especially more so when phylogenetic effect is minimized, WD was negatively related to tree mortality and d.b.h. increment, while a positive trend was observed between d.b.h. increment and tree mortality. A negative trend was also detected between maximum plant height and WWC, which was interpreted as a consequence of increased evaporative demand and use of xylem stored water by taller trees in order to compensate for hydraulic limitations to water transport induced by frictional resistance. No doubt, the traits chosen may vary spatially, but the consistent interspecific patterns observed in this study among coexisting species of differing adult stature reflect 'vertical' niche differentiation and may help to explain population regulation in a multispecies ecosystem like tropical rainforest.

Key words: brunei-borneo, comparative study, demography, life history strategy, species coexistence.

INTRODUCTION

Along with many other factors, the strong vertical light gradient in tropical rainforests invokes intense competition among coexisting trees for light and space and thus results in ecological specialization. This in turn is expected to lead to covariation across species in many life history characters including stem growth, wood-specific gravity/water content, tree mortality and lifespan/successional status (Thomas 1996; Turner 2001; Laurance *et al.* 2004), asymptotic height, assimilation rate, wind resistance and stability safety factors (Niklas 1994; Thomas 1996; Sterck & Bongers 1998).

One of the attributes mentioned above, wood-specific gravity (henceforth referred to as wood density), is a trait that is highly correlated with density of carbon per unit volume (see Muller-Landau 2004) and is of direct applied importance for estimating ecosystem carbon storage and fluxes (Fearnside 1997; Nelson *et al.* 1999; Wiemann & Williamson 2002). Through practical experience, foresters have found that wood density is linked to many commercial attributes of timber and is correlated with a number of important mechanical properties. For example, high wood density is an excellent support against gravity, buckling, wind, snow and other harsh environmental forces (Putz *et al.* 1983; Wiemann & Williamson 1989). Hacke *et al.* (2001) even showed that variations in wood density and structure are linked to prevention of xylem implosion (embolism) caused by negative pressure and suggested that trends in wood density may be as much or even more related to support of the xylem pipeline as to support of the plant. Yet, there is a dearth of information on how wood density varies both within and between species with other life history functions (but see Wiemann & Williamson 1989, 2002; Turner 2001; Muller-Landau 2004), such as with maximum (asymptotic) plant height, tree diameter size and growth rate, tree water content (storage

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capacity) and survival. We predict that, all else being equal, plants with low wood density should increase their volume faster in terms of height extension and/or diameter increment than those with high wood density. Furthermore, such fast growth will be at the expense of survival as species with low wood density lack enough structural reinforcement to ward off herbivores, pathogens and falling debris. Some studies have indicated that seedlings and juveniles with high wood density survive better, but grow less in the gloom of the forest than those with low wood density (see Augspurger 1984; Osunkoya *et al.* 1992, 1994; Osunkoya 1996; Walter & Reich 1996). King *et al.* (2005) contend that much of the observed variation in tree growth, both within and among species, can be related to two central factors: light intercepted by a tree and density of its wood. However only large stature tree species (height > 25 m) were considered in their studies, thus limiting the utility of such a generalization.

It is also often hypothesized that there should be systematic relationships between adult plant stature (e.g. maximum plant height) and ecophysiolgical traits (e.g. wood properties and hydraulic network of xylem fibres), particularly in a closed canopy system like the rainforest due to competition for light resource (Thomas 1996; Davies 2001; King *et al.* 2005). Thus, the growth and physiological traits of canopy/emergent species are expected to differ from those of understorey trees due to differences in their biomechanical requirements for structural support and life history strategy (Niklas 1994; Thomas 1996; Enquist *et al.* 1999; Poorter *et al.* 2003). However, many of these relationships or expected differences have rarely been investigated (but see King 1986; Aiba & Kohyama 1996; Thomas 1996; Phillips *et al.* 2003; Falster & Westoby 2005). Increase in plant height might call for increase in wood density and/or modulus of elasticity to increase stiffness (resistance to static and impact bending, compression and tension) in order to minimize buckling and the effect of wind stress prevalent above the canopy (see King 1986; O'brien *et al.* 1995). However, as density of dry cell wall material is more or less constant (reaching a maximum of 1.5 g cm^{-3}, see Roderick & Berry 2001), such an increase in wood mass per unit volume (i.e. density) would lead to a decline in the amount of space available for hydraulic network of the stems. Thus, if as trees get taller, increasing hydraulic conductance (e.g. procurement of large diameter xylem vessels for fluid transport and storage) is more important functionally to service the increasing living biomass (Thomas 1996; Phillips *et al.* 2003) than minimizing wind stress via increasing stiffness, then we hypothesize that a negative relationship should exist between wood density and maximum height. An extension to the above hypothesis is that as smaller stature tree species may be more subject to physical damage throughout their life spans due to the impact of falling woody materials and animal activities, such trees are expected to possess higher wood density than larger stature tree species.

The purpose of this paper is to examine across-species patterns of covariations among wood density, wood water content (WWC) (a surrogate of stem-water storage capacity), tree mortality, stem growth and maximal (asymptotic) height using 27 rainforest tree species of varying adult stature whose individuals are abundant within a 1-ha plot. We used data from a permanent forest plot setup for long-term studies of tree dynamics in Kuala Belalong rainforest, Brunei, on Borneo Island, South-east (SE) Asia (see Small *et al.* 2004). Within this plot, along with easily measurable traits of tree survival and growth, we determined tree wood density and WWC directly rather than relying on published values. This helps to increase the precision in the dataset, as wood density is known to vary among sites in relation to soil fertility, successional stage, rainfall and seasonality (Wiemann & Williamson 2002; Muller-Landau 2004). Additionally, WWC is rarely reported in the literature although always measured in determining oven-dried wood density values. Furthermore, in order to best infer functional relationship, we accounted for potential effects of phylogenetic relatedness by applying independent contrasts analyses (see Harvey & Pagel 1991; Garland *et al.* 1992).

METHODS

Study site

Data were collected from trees of Kuala Belalong mixed dipterocarp lowland rainforest, which is part of the Ulu Temburong National Park, Brunei Darussalam (4°30′N, 115°10′E). Mixed dipterocarp forests (MDF) with emergent trees up to 40–60 m tall are a well-represented forest formation in Brunei with Anacardiaceae, Euphorbiaceae, Dipterocarpaceae, Lauraceae, Myrtaceae and Rubiaceae being the dominant families (Ashton & Hall 1992; Ashton *et al.* 2004). The tropical forest of Belalong is extraordinarily species-rich (256 species ha^{-1}, Cranbrook & Edwards 1994; Small *et al.* 2004). The forest is similar in community structure to other lowland MDF in Borneo in that there is typically a lack of dominant species and the distributions of many main canopy/emergent species (often >40 m high) tend to be localized. In addition, many species are locally rare with <5 individuals ha^{-1}. The soils of the area are orthic acrisols derived from shale parent materials. They are relatively porous in bases and have clay enriched B-horizon with deep profiles up to 2 m in depth. Mean annual rainfall is approximately 5080 mm with no distinct dry season. Typical of an equatorial climate, the temperature has little variance with daily maximum between 30.5°C (January) and 35°C (March) and minima around 25°C.

In September 1995, a 1-ha unlogged MDF plot was set up in a low to mid-slope valley position, west of Belalong river in Kuala Belalong, by the Earthwatch Institute and the Universiti Brunei Darussalam (UBD) Kuala Belalong Field Studies Centre for the purpose of long-term study of tree population dynamics (see Small *et al.* 2004). All trees ≥5 cm diameter at breast height (d.b.h.) were taxonomically identified, mapped (using *x* and *y* coordinates), numbered with aluminium tags and measured for tree diameter at breast height (d.b.h.) at a red-paint mark usually 1.3 m above the forest floor; for trees with buttresses, d.b.h. measurement was taken 20 cm above the top of the buttress. Voucher specimens of all species identified were deposited in the herbaria of the Biology Department, UBD and Brunei Forestry Department. The topography is gently undulating in approximately half of the plot but is quite rugged in the remaining portion with some sections having 20–30 m elevational gradient, dissected by two streams and extensive ridge systems. There is no evidence of tree growth, mortality or species spatial distribution being significantly influenced by the topography (O. O. Osunkoya, unpubl. data 2004). Within the plot, 1019 individual trees >5 cm d.b.h. were identified from 278 species. Mean stem diameter of trees ≥5 cm d.b.h. in this plot is 12.8 cm with the upper range extending to 97.5 cm. However, the forest structure is marked by a few tall (>45 m) and hence a few large d.b.h. (>60 cm) emergents such as *Koompassia excelsa* (Caesalpiniaceae) and *Crypteronia griffithii* (Crypteroniaceae). Instead, lower understorey and midcanopy species dominate the plot with average height of all individuals over the hectare being 11 m (see Small *et al.* 2004 for details of the floristics of this plot).

Sampling procedure: tree height, mortality and d.b.h. increment

The 1-ha permanent plot was revisited in September 2004 to document mortality and changes in tree diameter for the entire 1019 individual plants (from 278 species). All tree individuals were relocated using the grid maps drawn earlier in 1995. Using diameter tapes, the surviving trees were remeasured at the 1995-paint mark for d.b.h. changes after loosening any epiphytes and lianas that might be present. Any previously tagged plant that could not be found was declared dead only after repeated search (≥3 attempts) of the plots using the tree coordinates and the map supplied. Using clinometers, tree height was determined for stems with less than 10° lean and with no evidence of past crown or stem damage or disease. For the present study we focused on 27 species (from 13 families) whose individuals are abundant ($n > 10$ individuals) in the 1-ha plot. For these selected species, maximum (potential) plant height ($H_{\max}$) was estimated as $H = H_{\max} \times [1 - \exp(-aD^{b})]$ where H is tree height in m, D is d.b.h. in cm and a and b are allometric coefficients that approach values of standard allometric constants for small values of H (see Thomas 1996). The species were then categorized into three adult stature groups of understorey (maximum height ≤15–20 m), midcanopy (maximum height, 20–30 m) and canopy/emergent (maximum height, >30 m) tree species. These species are listed in Table 1, together with their growth forms. Taxonomy follows Coode *et al.* (1996).

From the diameter measurements and tree census, tree diameter increment (δd) and mortality rates were calculated as:

$$\delta d = (D_t - D_0)/t\text{, and } m = 1 - (N_t/N_o)^{1/t},$$

where t = number of years between census (9 years), N_o = population number at first recording (1995), N_t = population number at t years (2004) and D = tree d.b.h.

Wood density and water content determination

We sampled wood from the outer into the inner portion of the trunk of living trees. For each of the 27 chosen species, a range of tree size was sampled (5–60 cm d.b.h.). The number of trees sampled per focal species varied, depending on the density of individual species in the 1-ha study plot, but in all cases, $n \geq 4$ trees per species (see Table 1). Short cylindrical cores, 30–100 mm long (depending on tree diameter) from the periphery into the inner portion of the trunk, were obtained at breast height (1.3 cm high) using a 5-mm-wide increment borer (SUUNTO, Vantaa, Finland). Two cores were taken per tree. In trees with buttresses, cores were taken from the stem portions in between two buttresses. Volume and fresh weight of each core sample were determined, usually within 24 h. The materials were then oven dried at 100°C for 7 days. Volume was determined by assuming the core is cylindrical and hence using $\pi r^2 h$, where r is the radius (2.5 mm) and h, is the length of the core sample (measured with a digital caliper). Wood density (specific gravity) was calculated as dry mass divided by fresh volume. Wood water content was derived from the ratio of the difference between wet and dry mass to the wet mass, and expressed as a percentage.

Statistical analyses

To examine covariation among the traits recorded, patterns were assessed (with and without phylogenetic

Table 1. Study species and mean values of the traits measured

Family and *species*	Growth Form	N (N_w)	Maximum height (m)	Wood density (g cm^{-3} ± SE)	Wood moisture (% ± SE)	d.b.h. increment (mm year^{-1}, 95% confidence limits)	Annual mortality (%)
Annonaceae							
Goniothalamus tapis	Understorey	14 (4)	15.51	0.469 ± 0.046	50.34 ± 5.25	1.22 (0.45–3.30)	4.94
Dilleniaceae							
Dillenia excelsa	Midcanopy	28 (11)	26.65	0.546 ± 0.020	51.91 ± 1.58	0.67 (0.41–1.08)	3.58
Dipterocarpaceae							
Shorea parvifolia	Emergent	12 (6)	53.10	0.336 ± 0.048	30.85 ± 3.71	2.68 (1.10–6.52)	3.33
Ebenaceae							
Diospyros borneensis	Understorey	25 (5)	18.10	0.583 ± 0.034	39.77 ± 2.62	0.95 (0.61–1.48)	2.00
Euphorbiaceae							
Aporusa elemeri	Understorey	33 (11)	18.01	0.580 ± 0.019	44.04 ± 1.66	0.75 (0.50–1.13)	2.36
Aporusa grandistipula	Understorey	15 (8)	20.03	0.654 ± 0.023	43.92 ± 1.85	0.78 (0.41–1.33)	0.74
Aporusa subcaudata	Understorey	12 (6)	17.52	0.626 ± 0.026	44.19 ± 2.14	0.54 (0.28–1.05)	0.00
Baccaurea racemosa	Midcanopy	16 (5)	23.16	0.571 ± 0.019	43.17 ± 2.35	0.86 (0.44–1.66)	4.86
Baccaurea trunciflora	Midcanopy	11 (4)	22.16	0.660 ± 0.046	41.58 ± 3.71	0.29 (0.11–0.78)	2.22
Glochidion rubra	Understorey	32 (4)	11.29	0.483 ± 0.045	53.62 ± 3.71	0.63 (0.15–2.56)	6.67
Macaranga hosei	Midcanopy	12 (5)	26.52	0.361 ± 0.034	48.50 ± 2.45	1.96 (0.72–5.28)	4.76
Malottus sp. 1	Midcanopy	22 (10)	29.34	0.633 ± 0.026	36.74 ± 1.66	0.76 (0.46–1.24)	3.03
Malottus ecaustus	Understorey	38 (22)	21.52	0.615 ± 0.014	37.81 ± 1.12	0.81 (0.56–1.17)	2.63
Malottus wrayi	Understorey	19 (4)	20.70	0.656 ± 0.032	39.04 ± 2.26	0.54 (0.32–0.89)	1.85
Neoscortechinia kingii	Midcanopy	14 (7)	26.10	0.591 ± 0.024	40.89 ± 1.98	1.38 (0.69–2.79)	3.97
Fabaceae							
Fordia sp. 3	Understorey	34 (20)	15.02	0.558 ± 0.015	49.08 ± 1.17	0.49 (0.33–0.71)	1.31
Fordia splendidissima	Understorey	31 (15)	14.79	0.574 ± 0.017	48.74 ± 1.36	0.74 (0.50–1.08)	0.71
Lauraceae							
Litsea oppositifolia	Midcanopy	27 (6)	25.60	0.596 ± 0.034	33.01 ± 2.62	1.14 (0.66–1.97)	4.44
Melastomataceae							
Pternandra coerulescens	Understorey	12 (5)	21.53	0.573 ± 0.037	45.89 ± 3.02	1.26 (0.56–2.82)	4.63
Myristicaceae							
Horsfieldia polyspherula	Canopy	25 (4)	34.04	0.552 ± 0.048	36.41 ± 3.71	1.49 (0.92–2.40)	3.20
Knema ashtonii	Canopy	49 (9)	45.78	0.550 ± 0.023	35.71 ± 1.75	1.56 (1.13–2.15)	1.11
Myrtaceae							
Syzygium caudatum	Emergent	24 (10)	35.12	0.634 ± 0.023	40.52 ± 3.71	1.08 (0.66–1.77)	1.85
Syzygium sp. 2	Canopy	27 (5)	35.90	0.737 ± 0.021	33.01 ± 1.66	0.98 (0.58–1.67)	1.53
Oleaceae							
Chionanthus spicatus	Understorey	14 (7)	20.69	0.619 ± 0.024	36.45 ± 1.46	0.94 (0.62–1.44)	1.23
Polygalaceae							
Xanthophyllum discolour	Midcanopy	18 (4)	23.67	0.628 ± 0.034	48.13 ± 2.62	1.36 (0.84–2.20)	1.11
Rubiaceae							
Urophyllum arboreum	Understorey	27 (8)	17.70	0.552 ± 0.023	47.85 ± 1.86	0.93 (0.53–1.65)	4.63
Ixora grandiflora	Understorey	13 (4)	17.15	0.705 ± 0.048	39.80 ± 3.71	0.58 (0.30–1.13)	1.0
Mean				0.594 ± 0.017	41.44 ± 1.19	1.05 (0.57–2.13)	2.73

N is the number of individuals >5 cm d.b.h. in the study plot, and were surveyed for stem growth and mortality. N_w is the number of individuals cored for wood density estimation.

effect consideration) using a series of univariate and multivariate techniques, including ANOVA, correlation and regression analyses. For each variable, data collected were checked for conformity with the assumptions underlying parametric tests. D.b.h. increment data were the only trait that did not achieve normality, and hence log transformed. D.b.h. increment values presented below have been back-transformed. For cross-species comparative analyses, each species contributes a single data point obtained by averaging values of all individuals of that species. Where necessary, significant differences between the means were tested at $P \leq 0.05$ using ANOVA or appropriate non-parametric tests. All data were analysed using SPSS (Version 12.0, SPSS Inc., Chicago, IL, USA).

A phylogenetic tree drawn to family level was constructed by hand for the 27 focal species using Soltis *et al.* (2000) as the backbone. Molecular studies of relationships within families and genera in Webb (2000) and Wurdack *et al.* (2005) helped to refine the drawn phylogeny down to genera/species level, especially for members within the Euphorbiaceae family (figure not shown). The independent contrast analyses method for continuous data was then employed to control for phylogenetic association in the dataset (Harvey & Pagel 1991) using the PHYLIP package of Felsenstein (2004). This method is now routinely used in comparative analysis, and readers are referred to the original reference for further details of the methods (Garland *et al.* 1992). Briefly, using the inferred phylogenetic tree, a contrast dataset is created, in which the value assigned to each contrast is calculated as the difference between the trait values for the two nodes, or species descending from the contrast node. Node values are themselves calculated as the average of trait values for the two immediately lower nodes or species. Each contrast is then scaled using information on the length of the branches leading from the node. The set of within-taxon contrasts were then analysed using standard regression techniques. All correlations between contrasts were forced through the origin (Garland *et al.* 1992).

RESULTS

General pattern of stem diameter increment

A total of 604 trees were surveyed, comprising approximately 60% of tagged trees in the study plot. Table 1 shows the mean data for the 27 species. Differences in stem diameter increment between species were highly significant ($P = 0.006$; Table 1). Lowest stem size increments (<1 mm year^{-1}) were recorded for species within the genera *Aporusa, Baccaurea, Glochidion, Malottus*, *Fordia*, *Ixora* and *Dillenia*. *Macaranga* and *Shorea* exhibited the highest stem growth increments (>2 mm year^{-1}), while growth of *Knema, Horsfieldia*, *Pternandra* and *Xanthophyllum* were intermediate. Overall, mean diameter increment for all trees >5 cm d.b.h. was 1.05 mm year^{-1}, and 1.32 mm year^{-1} when only trees >10 cm d.b.h. are considered.

General pattern of tree mortality

Size-class frequency distribution of surveyed trees is given in Figure 1a. Overall, tree mortality decreased exponentially with increase in tree d.b.h. size (using 1995 diameter data as the predictor variable; Fig. 1b). However, the proportion that died by 2004 (relative to 1995 tree abundance) was not significantly related to tree size-class as size distribution of dead trees mirrored 1995 tree size distribution ($\chi^2 = 0.56$, $P = 0.97$; Fig. 2b). Lowest annual mortality rates (approx. 1.0–1.5%) were recorded for species within the genera *Aporusa, Chionanthus*, *Fordia*, *Ixora*, *Knema* and *Xanthophyllum* (Table 1). The remaining species had moderate annual mortality (2–4.5% annually), except *Glochidion* that experienced annual mortality close to 7%. Across species, long-term average rate of tree mortality was 2.73% per year for all trees >5 cm d.b.h., and 1.16% per year if only trees >10 cm d.b.h. were considered.

General patterns of wood density and water content

A total of 209 trees were cored for wood density estimation. The majority of wood density values were in the range of 0.50–0.74 g cm^{-3}, except for *Goniothalamus tapis* (Annonaceae), *Shorea parviflora* (Dipterocarpaceae), *Macaranga hosei* and *Glochidion rubra* (both Euphorbiaceae) where lower values were recorded (Table 1). *Ixora grandiflora* (an understorey species) and *Syzygium* sp. 2 (a canopy species) exhibited the highest wood density among the 27 species investigated (see Table 1). Overall, although the range was minimal and hence the coefficient of variation was low (14.67% at species level), wood density varied appreciable among species ($F_{26,181} = 6.08$, $P < 0.001$).

Wood water contents were between 30 and 50% of the wood and differed significantly between species ($F_{26,208} = 9.31$, $P < 0.0001$) and with a comparable coefficient of variation (CV = 18.08%) to that of wood density (14.67%). *Dillenia excelsa, Goniothalamus tapis* and *Glochidion rubrum* exhibited the highest WWC (approx. 50%), while *Shorea parviflora* showed the lowest WWC (30.8%) despite its low wood density (0.336 g cm^{-3}) (Table 1).

Adult tree stature effect

Overall, wood density value for the canopy species was moderate (0.56 g cm^{-3}) while annual tree mortality was low (2.21% per year). However, these values were not statistically different from that obtained for the two lower stature species (Table 2). Diameter growth was statistically different between the three adult stature groups, and was in the order canopy > midcanopy > understorey species. The wood of canopy species contained significantly less moisture compared with the midcanopy and the understorey species (Table 2).

Interspecific correlations among life history traits

Figure 2 and Table 3 show the relationships among wood density, WWC, stem growth and mortality, and maximum tree height at the species level. Trends observed can be summarized as follows: across species, a significant negative relationship was found between wood density and tree mortality, such that species with high wood density experienced lower mortality (Fig. 2a); species with faster stem d.b.h. growth tended to have significantly lower wood density but higher mortality, albeit insignificant (Fig. 2b,c); no significant association could be detected between wood density and WWC, primarily because of an outlier (*Shorea*

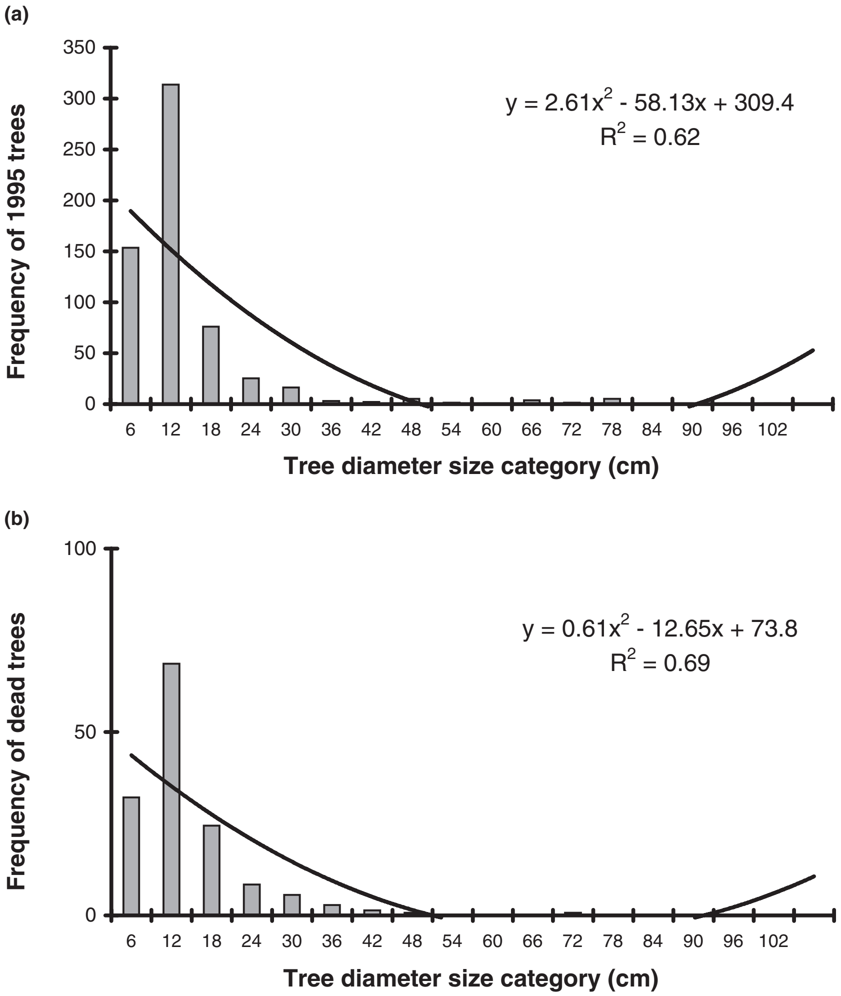

Fig. 1. Frequency distribution of diameter size for trees of 27 species whose individuals are abundant (>10) in a 1-ha plot in Kuala Belalong forest, Borneo: (a) alive individuals at the initiation of the permanent plot in 1995, and (b) dead individuals in 2004.

parvifolia) among the survey species (Fig. 2d); lastly, tree maximum height was not significantly related to wood density but was negatively correlated with WWC (Fig. 2e,f).

We also examined patterns of interspecific covariation among these attributes within the Euphorbiaceae – a family with the largest number of species (11) in the dataset. The patterns are also given in Figure 2 (open circle data points) and in Table 3. In all cases, trends described above were maintained and even reinforced as judged by the strengths of the relationships (r and R^2 values). Using the phylogenetic independent contrast method and thus minimizing the influence of phylogenetic membership on species dataset, most relationships described above were also found to remain significant and at times stronger (Table 3). Noteworthy is the tree mortality relationship with WWC which was not significant when species was used as independent data point ($r = 0.27$, $P = 0.17$) but now appeared significant ($r = 0.43$, $P = 0.03$).

DISCUSSION

Observed life history patterns compared with the rest of the world

Overall, our sampling effort covered varying tree adult statures. For the 27 species examined, mean diameter increment for all trees >5 cm d.b.h. was 1.05 mm year^{-1} (95% CI: 0.57–2.13 mm year^{-1}). When only trees >10 cm d.b.h. are considered, as in most studies around the globe, d.b.h. increment, considering all surviving individuals of targeted trees,

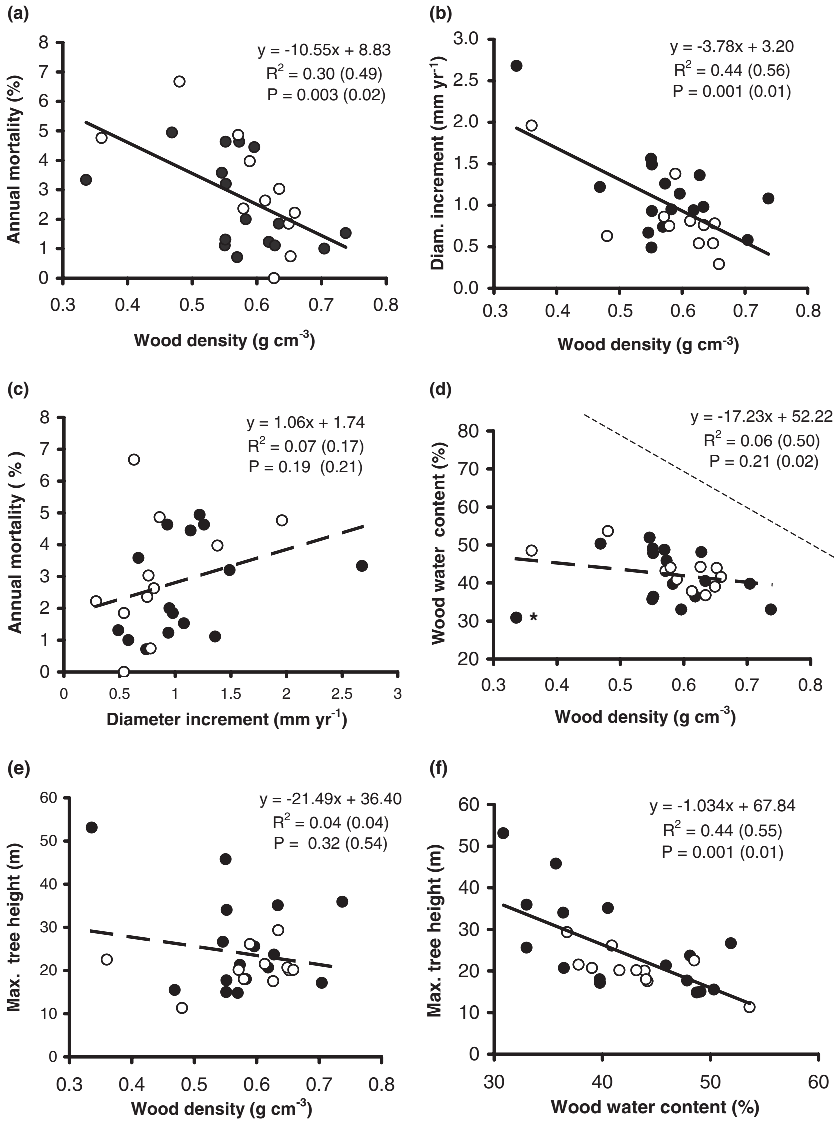

Fig. 2. Patterns of covariation among plant traits using species as independent data points: (a) stem mortality *versus* wood density (WD); (b) stem growth *versus* WD; (c) stem mortality *versus* stem growth; (d) wood water content (WWC) *versus* WD; (e) Maximum tree height *versus* WD; and (f) maximum tree height *versus* WWC. Open circles distinguished data points for species within the Euphorbiaceae family. R^2 and P are coefficient of determination and significant (probability) values, respectively, for the entire 27 species and in parentheses for species within the Euphorbiaceae only. Significant trends for the 27 species are indicated by the heavy continuous lines ($P < 0.05$), and non-significant trends by the heavy broken lines. For the WWC–WD relationship, the faint dash line shows tree wood whose open space is saturated with water (i.e. WD = 1.5, WWC = 0; and WD = 0, WWC = 100%). The point with asterisk in the WWC–WD relationship is for *Shorea parvifolia* whose wood is light and appeared to be filled more with air that with water.

was 1.32 mm year^{-1} (95% CI: 0.52–2.65 mm year^{-1}). These values are within the range reported for some South American rainforests (e.g. Da-Silva *et al.* 2002; Laurance *et al.* 2004). However, the upper range appeared slightly lower compared with the range of stem d.b.h. increments found for forest trees in other parts of SE Asia (0.4–4.7 mm year^{-1}: Ashton & Hall 1992; Condit *et al.* 1999) and in other tropical regions (1.1–11.4 mm year^{-1}: Schmidt & Weaver 1981; Korning & Balslev 1994; Laurance *et al.* 2004). This might be due to the prevalence of understorey and midcanopy species and thus lack of many large size trees in the plot we studied; for example, only 28 out of 604 trees of the 27 species we used in this study have d.b.h. > 40 cm. The mean annual tree mortality for trees >5 cm d.b.h. was 2.73% (see Table 1). Again, after concentrating on trees >10 cm d.b.h., mean tree mortality of 1.16% per year is obtained. This is similar to that recorded for rainforests in other parts of SE Asia (Ashton & Hall 1992; Condit *et al.* 1999;

Table 2. Mean (±SE) trait values for different adult stature classes of rainforest trees species from Kuala Belalong, Brunei, Borneo

	Tree adult stature				
Variable	Understorey ($n = 14$)	Midcanopy ($n = 8$)	Canopy/emergent ($n = 5$)	F-ratio	P-value
Wood density (g cm^{-3})	0.591 ± 0.02	0.559 ± 0.04	0.562 ± 0.04	0.37	0.70
Wood water content (%)	44.08 ± 1.35	43.20 ± 2.20	35.30 ± 2.41	5.19	0.01
d.b.h. increment (mm year^{-1})	0.77 ± 0.10	1.21 ± 0.17	1.56 ± 0.18	8.12	0.002
Tree mortality ($\text{\% year}^{-1}$)	2.61 ± 0.42	3.48 ± 0.69	2.21 ± 0.76	0.87	0.43

N is the number of species per group.

Table 3. Cross-species correlation coefficients (*r*) among the five ecological attributes investigated

	Wood density	Wood water content	D.b.h. increment	Tree mortality	Tree maximum height
Wood density	–	−0.25 (−0.71*)	−0.66*** (−0.75**)	−0.56** (0.70*)	0.20 (0.21)
Wood water content	−0.28	–	−0.33 (0.22)	0.27 (0.51)	−0.67*** (−0.74**)
D.b.h. increment	−0.72**	−0.24	–	0.26 (0.41)	0.69*** (0.36)
Tree mortality	−0.62**	0.43*	0.35	–	0.09 (−0.16)
Tree maximum height	−0.24	−0.61**	0.64***	−0.20	–

*$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$. See Fig. 2 for the pattern/trends. Above the diagonal are the correlations at species level using the 27 species (d.f. = 25), and in parentheses are correlations within the 11 members of Euphorbiaceae family only (d.f. = 9). Below the diagonal are the correlations following removal of phylogenetic relatedness from species mean data (using phylogenetic independent contrasts method), and thus represents relationships that are minimized from phylogenetic influence.

Newbery *et al.* 1999) but appeared much lower than those in rainforests of other continents, especially South America (1.77–2.55% per year: Swaine *et al.* 1987; Lang & Knight 1983; Condit *et al.* 1999). Prevalence of seasonal and severe droughts has been implicated for the relatively high mortality in rainforests of South America, a phenomenon that is not as common in SE Asian rainforests (see Condit *et al.* 1995, 1999). It has to be noted although that comparison with other sites in the tropics has many difficulties given the huge range of conditions, methods of measurement, time of study, minimum d.b.h. of trees enumerated and community composition.

The density of wood is a measure that equates to wood quality and reflects the partitioning of carbon within the tree. Only the outer portion of the trunk was sampled in this survey. It is quite possible that this could have biased some of the estimates as wood density values have been shown to vary significantly in response to radial position – being generally higher in the sapwood (close to the bark) compared with the heartwood (pith) (Wiemann & Williamson 1989; McDonald *et al.* 1995; Cordero & Kanninen 2002). Also, trends in radial increase may vary in relation to successional status of a plant species: early successional (pioneer) species show radial increase in wood density towards the periphery while late succession species showed the opposite trend (McDonald *et al.* 1995; Woodcock & Shier 2002). Nonetheless, the wood density values (mean: 0.59 ± 0.02 g cm^{-3}; Table 1) reported in this study, although with a low coefficient of variation at species level (14.7%), are similar to those reported for other lowland forest in Borneo (Kalimantan: 0.58, Suzuki 1999) and for other rainforest trees around the globe (0.55 in Amazonian, Laurance *et al.* 2004; 0.58 in Cameroon, Worbes *et al.* 2003).

Covariation among life history traits

As hypothesized, across species, wood density was negatively correlated with stem d.b.h. increment (Fig. 2b and Table 3), suggesting that low wood density permits rapid growth, especially in larger stature tree species (Table 2). Similar trade-off between stem wood density and stem growth has been inferred (albeit indirectly) in the literature although evidence is scanty (see Putz *et al.* 1983; Enquist *et al.* 1999; Turner 2001; Muller-Landau 2004). However, the predictive power of this relationship was only moderate ($R^2 = 0.44$), suggesting that other factors such as tree light interception/environment and crown traits might influence the trade-off trend. Indeed King *et al.* (2005) showed that a combination of species crown light index, crown area and wood density explained tree growth far better in two Malaysian rainforests ($R^2 = 0.69$) than any of these three variables independently. Wood density, apart from being a measure of wood quality and carbon partitioning within a tree, is also a measure of the degree to which wood organs are protected from attacks by pests and pathogens and tree ability to withstand falling debris (or to resprout following damage), especially in the understorey environment. Hence, wood density is expected to covary negatively with tree mortality (Suzuki 1999; Turner 2001), as was found in this study (Fig. 2a). The significant negative trend also supports the assertion that fast-growing, shade intolerant species (e.g. *Malottus hosei, Shorea parvifolia* and *Glochidion rubra*) have low wood density and high mortality, whereas the wood of slow growing shade tolerant species (e.g. *Aporusa subcaudata, Ixora grandiflora, Xanthophyllum discolour* and *Fordia splendidissima*) is dense and associated with low mortality (Thomas 1996; Walter & Reich 1996; Davies 2001).

Roderick and Berry (2001) contend that the density of material in dry cell walls is more or less constant across species, reaching a maximum at ca 1.5 g cm^{-3}. Consequently, as the volumetric fraction of the cell-wall material increases with wood (cellulose and lignin), that of the remaining space (which is filled with either water or air) must decline concomitantly, leading to a negative relationship between wood density and WWC or air. This expected negative relationship was not observed in this study, primarily because of an outlier species – *Shorea Parvifolia* – in the dataset (Fig. 2d); the trend is significant when only the monophyletic group of Euphorbiaceae is considered ($R^2 = 0.50$, $P = 0.02$). Indeed, if the open space is completely filled with water, the wood density–WWC relationship will have a coefficient of 1.5 (faint dashed-line in Fig. 2d). The difference between this line and the point of each species in vertical direction shows the fractional volume occupied by air (see also Suzuki 1999; Gartner *et al.* 2004; Berry & Roderick 2005). Thus, species with less dense wood have more air in their open space than species with denser wood. Noteworthy is the wood of *Shorea parvifolia* that is low in density and seems filled more with air than water. Indeed, we observed the wood of this species to be quite spongy and brittle. The low density wood is thought to allow *Shorea* species to achieve increasing stem d.b.h and volume growth (see Table 1) especially at early stage, although they then switch to dense, non-spongy wood at a later stage in order to reduce mortality and attain longer life span than those of typical pioneers like the *Macaranga* (Suzuki 1999).

Contrary to our hypothesis (see the *introduction*), with or without phylogenetic influence, we found a loose association between wood density and maximum tree height (Fig. 2e; Table 3). This is also in contrast to the finding by Thomas (1996) who reported a negative trend between maximum plant height and wood density among 38 species from a few (six) genera in a Malaysian rainforest. Thus, this relationship requires more investigation. The negative relationship between maximum tree height and WWC as observed in this study (see Fig. 2f) has often been interpreted as a response and/or consequence of higher evaporative demand and increase use of xylem stored water by taller trees. This is to compensate for hydraulic limitations (in taller trees) to water transport induced by frictional resistance, a phenomenon that in itself increases with path length (tree height and branch length) and gravity (Phillips *et al.* 2003). It remains to be seen how widespread this trade-off is in non-seasonal evergreen tropical forests like the site we studied where severity of hydraulic limitation can be expected to be minimal.

CONCLUSION

The interspecific differences observed in this study reflect 'vertical' niche differentiation and may help to explain regulation in a multispecies system. The fact that some functional traits (wood density and moisture content) are significantly negatively correlated with demographic parameters (e.g. tree maximum height, d.b.h. growth and mortality) is a strong indication of physiological trade-offs. This agrees with Kohyama (1993) and Aiba and Kohyama (1996) that the term 'architectural syndrome' should be used alongside that of demographic/ecological syndrome to explain species coexistence in rainforests. Many of these interspecific variations are equally seen as trait differences between life history groups (see Table 2). To that extent, consistent significant differences in these traits were detected between small, medium and large adult stature plants. The weak explanatory power in some of these associations (e.g. annual mortality *vs* d.b.h. increment and wood density *vs* WWC) may be because of the low sample size in some of our dataset. It may also indicate that these chosen variables are imperfect indicators of life history strategy since they are greatly influenced by resource levels, which may vary stochastically among individuals and systematically between species (Muller-Landau 2004). No doubt, evolutionary relatedness may confound some of the patterns one is seeking. In this study, we have controlled for phylogenetic autocorrelation using the independent contrasts method. Nonetheless, future studies need not discard this influence. Instead as phylogenetic relationships and cladograms become highly resolved, we should heed Westoby *et al.* (1995) and Desdevises *et al.* (2003) advice by: (i) testing *a priori* hypotheses about pairs of variables without attempting to take account of cross correlations with other variables, like phylogeny (as was predominantly done in this study); and (ii) quantifying each of the three components of variation in the dataset, viz ecology, phylogeny and possible interactions, and recognizing their interpretations as complimentary rather than mutually exclusive.

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