Trees approach gravitational limits to height in tall lowland forests of Malaysia

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Summary

1. In the absence of wind, tree height is limited by elastic instability, which occurs when a tree becomes too spindly to erect itself when bent from the vertical. To assess the extent to which trees approach this limit and characterize species stature in diverse tropical forests, we measured tree dimensions in tall, dense forests at Lambir Hills, National Park, Sarawak, Malaysia and Pasoh Forest Reserve, Peninsular Malaysia. From these measurements we determined characteristic adult heights and trunk diameters for 91 species.

2. Across all species, adult height scaled with adult diameter to the 2/3 power, as predicted for a column at its buckling limit. These heights were, on average, 65% of the buckling limit calculated for a cylindrical column with typical wood properties.

3. At a given diameter, the species of Lambir were 9% taller than those of Pasoh, a pattern related to the greater rainfall and density of trees at Lambir.

4. On the topographically rugged Lambir plot, large emergent trees were shorter on ridges than in hollows, whereas small, sheltered trees showed no relation between allometry and elevation.

5. Thus, trees may approach gravitational limits to height in favourable environments for growth where there are large advantages of height for light interception and trees are sheltered from wind.

Key-words: mechanical limits to height, tree allometry, tree architecture, tropical forest

Introduction

The relationship between tree height and trunk diameter has been of interest ever since McMahon's (1973) oft-cited study of the proportions of trees in relation to the limits imposed by mechanical support requirements. The extent to which trees approach these limits affects the cost in biomass of reaching a given position in the forest canopy and hence is of broad significance (Givnish 1995; Aiba & Nakashizuka 2007). For a slender, erect, column of given composition that is fixed at the base, maximum height is proportional to column diameter to the 2/3 power. When this maximum height is exceeded the column bends over due to elastic instability, which occurs when the restoring force exerted by the column is insufficient to counter the bending torque exerted by the column's weight when it is deflected from the vertical. Consistent with this buckling limit, McMahon (1973) found that height was roughly proportional to the 2/3 power of trunk diameter at breast height (1·37 m) across record-sized trees of hundreds of species, ranging from 2 to 110 m in height. However, these

trees were, on average, only one-fourth as tall as the buckling height and showed substantial residual variation about the 2/3 power relation between height and diameter.

Subsequent studies have shown that forest-grown trees commonly deviate from this 2/3 power relationship, though they may conform to it over an intermediate size range (King 1986; 1996; Farnsworth & Niklas 1995; Osunkoya *et al.* 2007). Height is roughly proportional to diameter among understorey saplings, but increases more gradually among large canopy trees (Kira 1978; Sterck & Bongers 1998). These shifts in allometry support the use of asymptotic functions of the form $1/H = 1/(aD + H_{max})$ in describing height–diameter relationships within particular forests (Kira 1978; Thomas 1996). Nonetheless, most forest trees lie considerably closer to the buckling limit than do record-sized trees, identified primarily based on their extreme girths and broad crowns.

Tree allometry also varies in relation to environment. Widely spaced, open-grown trees have trunks that are several times as thick as those of forest-grown trees of similar height (Ek 1974; King 1981). Trees of wind-exposed ridges are shorter and squatter than those of more sheltered slopes (Lawton 1982). In contrast, trees that are prevented from

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swaying by guy wires grow to be more slender than freely swaying trees (Jacobs 1954). Holbrook & Putz (1989) found that *Liquidambar styraciflua* saplings that were both guy-wired and shaded from the sides grew nearly twice as fast in height as the open-grown controls, but often buckled under their own weight when their supports were removed. Thus, the extent to which trees approach buckling limits to height varies considerably, depending on crown size, exposure to wind and light, crowding by neighbours and stage of development.

Tree height–diameter relations are also of interest in the quest to characterize the heights to which co-occurring species grow. Recent studies of tropical forests have identified maximum height as a correlate of the architectural, physiological and demographic traits of co-existing species (Thomas 1996; Thomas & Bazzaz 1999; Kohyama *et al.* 2003; Poorter *et al.* 2003, 2006; Bohlman & O'Brien 2006). Diversification in adult height and associated traits both within genera and across broader taxonomic scales may contribute to species co-existence (Thomas 1996; Kohyama *et al.* 2003; King *et al.* 2006c), along with other factors, such as density-dependent growth and recruitment (e.g. Wright 2002).

The characterization of adult height for species of diverse tropical forests is a daunting task. In a few cases, plot-wide measurements of height have been used to estimate the maximum heights of the more common species (e.g. Poorter *et al.* 2003). In other instances, height–diameter curves have been constructed from samples of trees allowing maximum height to be estimated from measures of maximum diameter (Thomas 2003). As tree diameters are routinely measured on research plots, this method has great potential for characterizing the adult stature of trees. However, the accuracy of the method is uncertain, as height–diameter relations for forest-wide samples (often dominated by juveniles) may differ from those restricted to adult trees of differing stature.

To characterize adult tree heights and assess the extent to which trees approach buckling limits to height on a forest-wide basis, we conducted a comprehensive study of the adult heights of 91 species on two large-scale forest dynamics plots in tall lowland forests of Malaysia. The great height of the dipterocarp-dominated forests of Malaysia and other parts of Borneo and Sumatra may favour low buckling safety factors by sheltering trees from wind and selecting for height growth to increase access to light.

Materials and methods

SITES AND SPECIES

The study was conducted in lowland forests dominated by Dipterocarpaceae on two forest research plots of 50 and 52 ha, respectively, at Pasoh Forest Reserve, Peninsular Malaysia (2°59′N, 102°18′E) (Manokaran *et al.* 2004) and Lambir Hills National Park, Sarawak, Malaysia (northwest Borneo) (4°12′N, 114°01′E) (Lee *et al.* 2004). The sites receive relatively evenly distributed rainfall, averaging 1800 mm year^{-1} at Pasoh and 2700 mm year^{-1} at Lambir, although prolonged droughts can occur during El Niño years (Lee *et al.* 2004; Manokaran *et al.* 2004). Most of the Pasoh plot is on a level alluvial plain *c.* 100 m a.s.l., whereas the Lambir plot includes varying

slopes, ravines and ridges ranging from 104 to 244 m a.s.l.. Sandy soils underlie the upper elevations of the Lambir plot, while more clay rich soils are common over the lower elevations (Lee *et al.* 2004). In both plots, all trees ≥ 1 cm diameter at 1·3 m height have been mapped, tagged and identified and tree diameters measured to the nearest 1 mm every 5 years (Condit 1998).

Species were selected over the full range in adult size and included the most abundant species on both plots. Forty species from 20 taxonomic families were measured at Pasoh and 55 species from 22 families at Lambir, including two subspecies of one species (Appendix S1). Four species were measured on both plots. The study species included 35% and 34% of all trees ≥ 1 cm diameter at Pasoh and Lambir, respectively.

CHARACTERIZATION OF ADULT HEIGHT AND DIAMETER

The specification of adult tree dimensions is uncertain due to variation in sample size and the fraction of trees above the size threshold used to choose samples. Previous estimates of maximum height include the asymptotic height of Thomas (1996) and the 95th percentile of height for trees above a fixed diameter threshold (Kohyama *et al.* 2003; Poorter *et al.* 2003). However, both methods require measurement of large numbers of trees and the latter method suffers from biases inherent in a fixed diameter threshold. The conventional threshold of 10 cm omits small species, whereas lower thresholds include many juveniles, so that the 95th percentile corresponds to subadult trees for large species.

To circumvent this bias we used the species-specific diameter threshold of King *et al.* (2006a), which includes only those trees that are ≥ 0·1 times the diameter of the thickest tree encountered for the species of interest. The 95th percentile of diameter was calculated for this sample and taken to be the characteristic adult diameter (D_A) for the species, a measure that is relatively insensitive to sample size and the presence of misidentified outliers (King *et al.* 2006a).

We restricted our samples to mature adult trees, as follows. Height was measured for trees of diameter ≥ 0·75 D_A, as encountered along lines of 20 × 20 m quadrats for each selected species. The characteristic adult height (H_A) for a tree of adult diameter (D_A) was determined from linear regressions of height vs. diameter for each species after excluding trees with substantial crown damage or dieback, or old stem breaks where the above-break diameter was < 0·75 times the below-break diameter. A few smaller trees with their crowns firmly entangled in neighbouring trees, and hence not self-supporting, were also excluded. H_A was determined from 4 to 18 trees per species per site (mean = 10·1).

For these purposes, tree height was calculated trigonometrically from measurements of distances and viewing angles to the highest point and the tree base. Repeated measurements of height with a Nikon 600 laser rangefinder insured that the highest point was measured for trees > 15 m tall. Heights were also corrected for a 0·5 m bias in our rangefinder's distance readings. Shorter trees were measured with an optical rangefinder – or folding rule if < 4 m tall. Viewing angles were determined by clinometer. For trees < 60 cm in diameter, trunk diameter was measured at the marked point used in previous censuses, unless this point was out of reach (above 2·2 m). For the latter trees and trees > 60 cm, diameter measurements of the last census were used (4–5 years ago for Pasoh and 2–3 years ago for Lambir). As large trees grow 0·4–0·5 cm year^{-1} on average at Pasoh (King *et al.* 2006a), this bias in diameter is relatively small.

The census protocol of measuring trees above any buttresses or obvious basal swelling or at 1·3 m, whichever point was lower,

resulted in diameter being measured at 1·3 m for nearly all trees < 30 cm in diameter and > 2 m for most trees > 60 cm in diameter. This avoidance of buttresses and butt swell minimizes the inflation of diameter that occurs when large trees are measured at the traditional breast height Van Pelt (2001).

ANALYSIS

The measured trees were compared to the height of instability (buckling limit) for a cylindrical column, calculated as (Greenhill 1881),

$$H_{cr} = 0.792(E/G\rho_g)^{1/3}D^{2/3} \qquad \text{eqn 1}$$

where E is Young's modulus of elasticity, G is the gravitational force per unit mass at Earth's surface (9·8 N kg⁻¹), ρ_g is the density of green (freshly cut) wood, and D is column diameter. Young's modulus denotes the resistance of wood to stretching or compression parallel to the trunk and is closely associated with resistance to bending. For 15 Southeast Asian woods commonly imported into the USA, mean $E = 10\,850$ MPa (i.e., 10.85×10^9 N m⁻²) (US Department of Agriculture 1999). For the 284 Bornean species studied by Suzuki (1999), mean green wood density = 980 kg m⁻³. Use of these values yields $H_{cr} = 82.5\,D^{2/3}$, when both height and diameter are specified in metres, or $H_{cr} = 3.83\,D^{2/3}$ for the usual convention of specifying tree diameter in centimetres and height in metres.

As buckling safety factors have been reported in terms of trunk diameter, as well as height, it is useful to rearrange eqn 1 to define the minimum diameter D_{cr} required to prevent elastic instability in a column of height H. For the chosen values of Young's modulus and green wood density, $D_{cr} = 0.001335\,H^{3/2}$, when both diameter and height are specified in metres, or $D_{cr} = 0.1335\,H^{3/2}$, when tree diameter is given in centimetres and height in metres. Height and diameter safety factors, expressed as ratios of actual to critical buckling dimensions, are related by $D/D_{cr} = (H_{cr}/H)^{3/2}$.

There was a slight difference in the height–diameter relations for large vs. small trees, based on examination of log-transformed plots of height vs. diameter. Hence, we split the data at 20 cm diameter, the approximate midpoint of the log-transformed distribution. As there are irregularities in both height and diameter and neither variate can be clearly defined as dependent vs. independent, we used standardized major axis (SMA) regression to compare the observed slopes to the slope of 2/3 predicted for trees at the buckling limit – and for between group comparisons. The SMA slope (= ordinary regression slope/r), minimizes the variance perpendicular to the fit line, after transformation so that var y = var x (Ricker 1984). SMA slopes were compared using SMATR version 2 (Warton *et al.* 2006).

Results

The measured trees were generally shorter than the buckling heights, but by rather small margins (Fig. 1). A few trees slightly exceeded this estimated limit on the Lambir plot, as did two excluded trees on the Pasoh plot, which were firmly entangled in neighbouring trees. However, most of the excluded trees were shorter than average and had been excluded because of past stem breakage. Among the non-excluded trees, log height was strongly correlated with log trunk diameter ($r^2 = 0.944$, Table 1). Half of the remaining residual variation was associated with differences between species within each site. Thus, there were highly significant differences among species, as well as between sites, but these
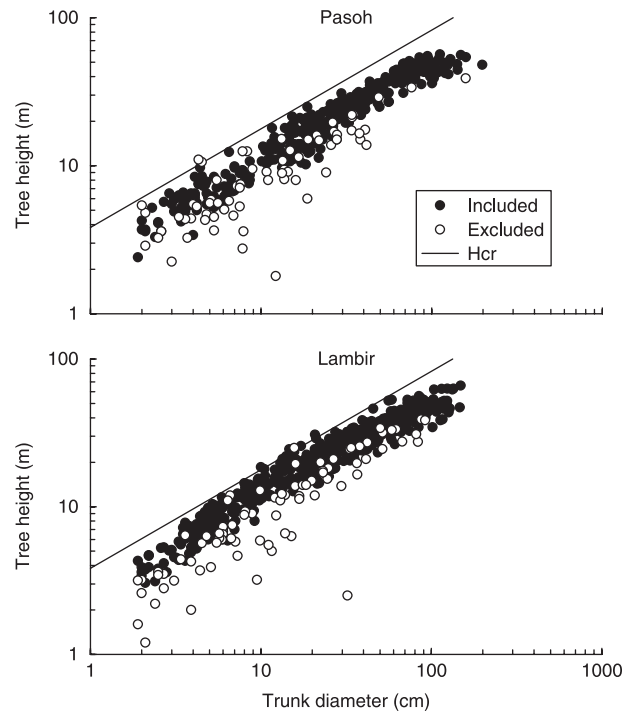

Fig. 1. Tree height vs. trunk diameter for adult trees on the forest dynamics plots at Pasoh Forest Reserve, Peninsular Malaysia and Lambir Hills National Park, Sarawak, Malaysia. The lines indicate the calculated critical height at which buckling would occur for a cylindrical column with the typical wood properties of live tropical trees. Excluded trees showed evidence of past stem breakage or crown damage or were entangled in the crowns of neighbours.

Table 1. ANCOVA of log tree height vs. log trunk diameter with site and species as factors, for non-excluded adult trees

Source of variation	d.f.	SSx/SS total	P
Log diameter	1	0·9441	$< 10^{-15}$
Site	1	0·0041	$< 10^{-15}$
Species	94	0·0272	$< 10^{-15}$
Log diameter × site	1	0·00004	0·192
Log diameter × species	94	0·0047	0·0000015
Residuals	780	0·0200	

Degrees of freedom (d.f.), proportion of the explained variance (SSx/SS total) and significance of the covariate, factors and interactions are indicated. Species refer to different species on each site, except for two subspecies of one species at Lambir.

differences were quite small compared to the variation in height over the sampled 100-fold range in diameter (Table 1).

The characteristic adult height H_A associated with the characteristic adult diameter D_A was below the buckling limit by at least 12% for each species (Fig. 2, Appendix S1). Log H_A was strongly correlated with log D_A ($r = 0.985$) across all species on the two plots, although the relationship was still slightly nonlinear. The SMA regression slope for species of $D_A < 20$ cm was slightly, but significantly greater than that for species of $D_A \geq 20$ cm (Table 2). For species of all sizes considered together, the two sites had a common SMA slope,
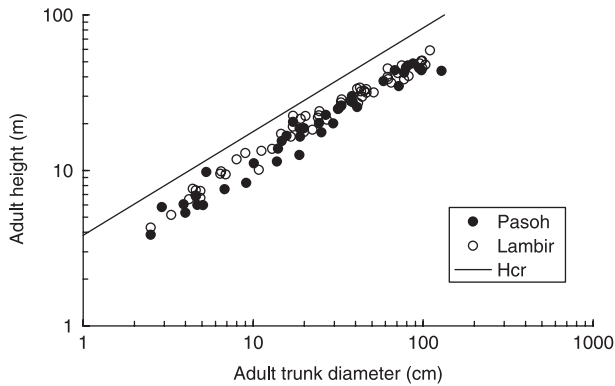
Fig. 2. Characteristic adult height vs. characteristic adult diameter for trees of 96 populations (91 species, four measured on both sites and two subspecies of one species).

Fig. 3. Tree height vs. stem diameter for trees at low elevations (106–160 m) vs. high elevations (210–242 m) on the Lambir plot. (Data not transformed to more clearly illustrate the between-group differences for large trees.)

Table 2. Standardized major axis regression relations between log (characteristic adult height) and log (characteristic adult trunk diameter) per species

Group	RMA slope ± SD	$H_A (D_A = 20$ cm) (m)	r	N
All species	0·659 ± 0·012	18·1	0·985	96
Species of $D_A < 20$ cm	0·733 ± 0·035*	19·5	0·954	42
Species of $D_A \geq 20$ cm	0·611 ± 0·026*	18·8	0·951	54
Pasoh species	0·667 ± 0·020	17·2	0·983	40
Lambir species	0·646 ± 0·013	18·8	0·989	56

The asterisks indicate significant differences in slope between large and small species ($P < 0.01$ and $P < 0.05$ after Bonferroni correction for five comparisons) and differences from a slope of 2/3 that are significant at $P < 0.05$, but not after correction for multiple comparisons. The other slopes were not significantly different from 2/3 or each other. Adult heights for a trunk diameter of 20 cm derived from the RMA regressions are shown for comparison and to allow reconstruction of the fit lines.

but the species of Lambir were 9% taller than those of Pasoh ($P = 0.0007$). The SMA slope of 0·659 for all species considered together was extremely close to the value of 2/3 defining the buckling limit.

On average, H_A was 65% of the estimated buckling limit (H_{cr}), a ratio that appears small in Fig. 2, due to compression associated with the logarithmic scale. Buckling safety factors expressed in terms of heights and diameters, respectively, were mean $H_{cr}/H_A = 1.57$ and mean $D_A/D_{cr} = 1.98$. Note that the mean of H_{cr}/H_A differs slightly from the reciprocal of the mean of H_A/H_{cr} and the mean of D_A/D_{cr} differs slightly from the mean of H_{cr}/H_A raised to the 3/2 power. These quantities would be identical, had geometric means been taken.

For the rugged Lambir plot, there was a significant effect of elevation on the relation between log height and log diameter for non-excluded trees of diameter ≥ 20 cm, including a significant diameter-elevation interaction, as determined by ANCOVA. The influence of elevation on tree height increased with diameter, as shown in Fig. 3, which compares trees at elevations of 210–242 m (on upper slopes and ridges) with
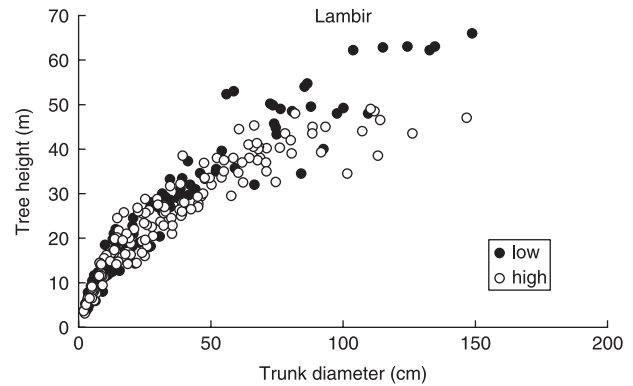
trees at elevations of 106–160 m (on lower slopes and in hollows). There was no relation between height and elevation for trees < 20 cm in diameter.

However, the relationship between height and diameter for trees of all sizes differed noticeably from the relation between adult height and adult diameter for five of the seven large-statured species for which juveniles were measured (Fig. 4). The height–diameter relations for large emergent species were somewhat log–log curvilinear, with juveniles often taller than adults of smaller statured species. Two of the species showing this pattern, *Dipterocarpus cornutus* and *D. globosus* had relatively small crowns in the pole stage (10–20 cm in diameter) but supported large crowns as emergent adults, as did most of the other emergent species. Thus, juveniles of certain large species approach the buckling limit more closely than do adult trees.

Discussion

Two noteworthy patterns were observed: (i) The relation between the characteristic adult height H_A and diameter D_A was very nearly log–log linear and quite close to the slope of 2/3 predicted for trees at the buckling limit. Slightly lower height–diameter power relationships were reported for a Panamanian forest by Muller-Landau *et al.* (2006) for 9043 trees of all sizes, also measured by laser rangefinder. (ii) Buckling safety factors for the measured trees were relatively small; observed H_A values were, on average, 65% of the estimated buckling heights. Even large emergent species followed this pattern. H_A was 59 ± 1·9% of the buckling height for the 12 species with $D_A > 80$ cm. Osunkoya *et al.* (2007) also observed low buckling safety factors, expressed as trunk diameter ratios, for a lowland forest in Brunei, Borneo.

Factors contributing to these patterns include our approach of comparing adults of different species, rather than trees of all sizes within species. Intraspecific height–diameter relations are often more curvilinear (Fig. 4; Fujimori 1977; King 1996; Thomas 1996; Poorter *et al.* 2006). In forests dominated by particularly long-lived species, large old trees
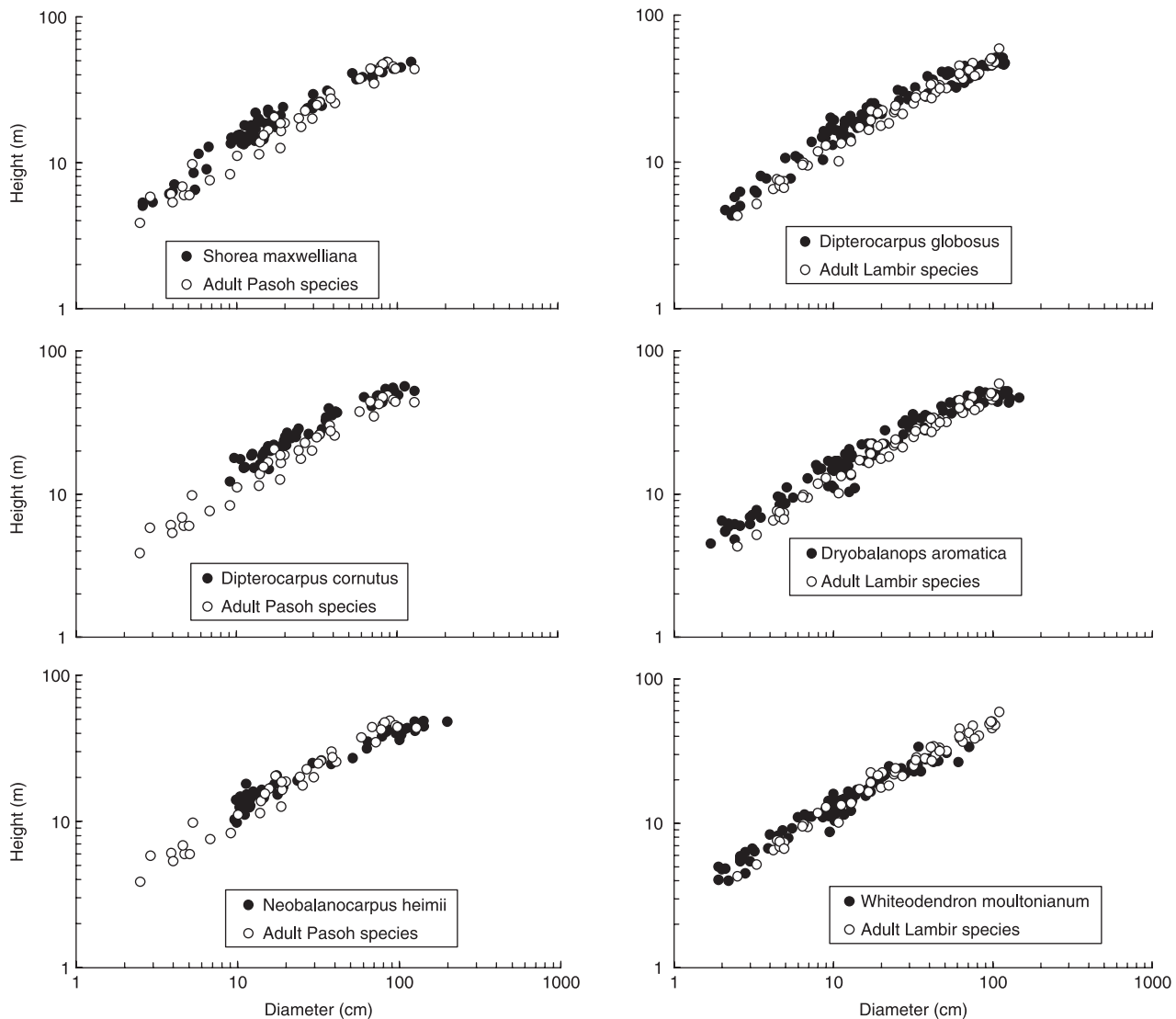
Fig. 4. Tree height vs. stem diameter for both juvenile and adult trees of six species, as compared to the characteristic adult tree dimensions for all measured species on the corresponding plot. Height–diameter relations for *Shorea leprosula* at Pasoh (not shown) were similar to those for *Dipterocarpus cornutus*.

may cease in height growth or show repeated top dieback and regrowth, while continuing to thicken their trunks (Ishii *et al*. 2000; Koch *et al*. 2004). This continuous diameter growth maintains young sapwood near the periphery, which is typically more conductive of water than older sapwood (Gartner & Meinzer 2005), and serves to overgrow and wall off wounds and decay (Schwarze *et al*. 2000). As a result of such cumulative diameter growth, most record-sized trees lie far below their estimated buckling heights (McMahon 1973).

The great height of lowland, dipterocarp-dominated forests of Borneo, Peninsular Malaysia and Sumatra may also favour low buckling safety factors by sheltering trees from wind and selecting for height growth to increase access to light. Forests of this region grow taller than those of Africa and the Neotropics (Richards 1996; de Gouvenain & Silander 2003) and both study sites have high densities of trees (LaFrankie *et al*. 2006). This greater forest height and high

tree density may be associated in part with the high recruitment of saplings of large trees in Southeast Asian forests, as compared to other tropical regions (LaFrankie *et al*. 2006). The slightly lower buckling safety factors for Lambir than Pasoh may be associated with higher rainfall and somewhat greater tree densities at Lambir, especially in the larger size classes (LaFrankie *et al*. 2006). In a study of pole-sized (10–20 cm d.b.h.) juveniles, King *et al*. (2005) found that trees of similar height tended to be narrower-crowned at Lambir than Pasoh.

The inverse relationship between tree height and elevation among large trees at Lambir (Fig. 3) suggests a link between tree dimensions and exposure to wind, as reported by Lawton (1982) for trees on vs. below the Continental divide at Monteverde, Costa Rica. In addition, trees on the sandy, well-drained ridgeline soils of Lambir are subject to more frequent water deficits, which may also limit their height growth (Koch *et al*. 2004).

The observation of a few free-standing trees that were slightly above the buckling limit (Fig. 1) may reflect variation in wood properties, trunk form and crown proportions that were not included in the calculation of buckling height. Wood properties affect the bucking height via the ratio of Young's modulus to green wood density, E/ρ_g (eqn 1). The buckling limit increases somewhat with green wood density, as associated increases in E outweigh smaller increases in ρ_g (Fournier *et al*. 2006; van Gelder *et al*. 2006). However, there is also substantial variation in wood moisture content among species (Suzuki 1999), which yields additional variation in ρ_g unrelated to E. It is plausible that E/ρ_g varies by at least twofold among our study species, which would result in a 1·26-fold range in the position of the buckling height line, as E/ρ_g is raised to the 1/3 power to calculate the buckling height (eqn 1).

The buckling height is also greater for tapered trunks, but decreases as an increasingly heavy crown is placed at the top. For a paraboloidal column with diameter $\propto L^{1/2}$, where L is distance below the tip, the buckling height is 1·35 times that for the cylindrical shape assumed here (Greenhill 1881). For a paraboloidal trunk with a crown of one-fifth of the trunk weight, centred at 0·9 times tree height, the buckling height is approximately equal to that for a cylindrical column (King & Loucks 1978). Note that the buckling equation for this form is given correctly by King (1981), but was misprinted by King (1986). If crown weight is decreased to one-tenth of trunk weight, the buckling height increases to 1·14 times that for an untapered column. The associated buckling relation passes above the heights of all measured trees – except for one of the juvenile *D. globosus* trees of Fig. 4.

Our finding that gravity may constrain tree proportions, is contrary to the conclusions of Niklas & Spatz (2004) that growth and hydraulic, rather than mechanical constraints, govern tree proportions. Niklas & Spatz (2004) based their conclusions on a general scaling model of growth, leaf biomass and stem diameter that predicted their observed log–log curvilinear relation for plants of various locales – when the model parameters were fit to this same data. Larger buckling safety factors have in fact been reported for small stems (< 2 cm d.b.h.), as determined by hanging weights on their crowns (King 1987; Niklas 1994). However, Niklas and Spatz' claim that their trees were an order of magnitude below the buckling limits reflects errors in plotting these limits, which were calculated correctly in their text.

Of course, our finding that trees of tall, dense forests of Malaysia show low buckling safety factors does not imply that these patterns are universal or that hydraulic constraints do not influence the growth of trees. Forests are shorter in areas of drier and more seasonal climates (Kira 1978) and in latitudes of 10–20° from the equator that are subject to hurricanes (de Gouvenain & Silander 2003). Canopy trees of such forests lie further below their buckling limits than those studied here (Kira 1978). The observations that wind-exposed trees have squatter trunks and that uprooting and stem breakage are important causes of tree death throughout the world (Putz *et al*. 1983; Franklin & DeBell 1988; Gale & Hall

2001) imply that strong winds also influence tree proportions. Frelich & Reich (1996) report that wood decaying fungi increasingly weaken the bases of trees, so that lower wind speeds are required to topple trees in forests that have gone for long intervals without strong winds. This synergism between decay and wind effects is probably widespread and helps to explain why old forests are more susceptible to catastrophic winds than young forests with sound wood (King 1986; Frelich & Reich 1996).

Trees often show partial stomatal closure during midday, implying that hydraulic conductivity limits photosynthesis (Roberts *et al*. 1990) and there is evidence that the anatomy of trees serves to optimize their hydraulic systems (McCulloh & Sperry 2005). The maximum height to which the tallest trees grow may be influenced by anatomical limitations to water transport, as affected by path-length resistance and gravity (Koch *et al*. 2004; Domec *et al*. 2008). However, lianas comprise roughly one-fifth of the leaf area of many tropical forests (Hegarty & Caballé 1991) and climb far above their buckling limits. Lianas have highly conductive stems due to their wide water-conducting vessels (Ewers *et al*. 1991). On the other hand, Santiago & Wright (2007) found lianas to have, on average, only 70% of the photosynthetic capacity of canopy trees in the exposed canopy of a wet Panamanian forest, suggesting greater hydraulic limitation of growth when support requirements are waived.

Thus, water transport requirements do not strictly limit height–diameter relations, at least in self-supporting angiosperms of wet tropical forests. Nonetheless, there are trade-offs between maximizing height growth under benign conditions in gap-dependent species with minimally designed, light-wooded stems and investing in sturdy, dense-wooded stems that can prevent both mechanical damage and xylem vessel collapse due to severe water deficits (Hacke *et al*. 2001; King *et al*. 2006b). In addition, the substantial amounts of wood required to support free standing trees may improve their capacity to withstand water shortages by increasing sapwood water reserves (Gartner & Meinzer 2005). The inference of low buckling safety factors in sheltered trees with narrow, crowded crowns and high safety factors in large crowned, open-grown trees exposed to greater wind forces and evaporative demand (Ek 1974) suggests that trees adjust their proportions in an adaptive fashion to meet varying requirements both for support and water transport.

Regarding the question of using adult trunk diameter to characterize adult tree height, this study suggests that simple power relationships of the form $H_A = aD_A^b$ may be adequate for this purpose. However, the coefficients a and b will vary among forests and the power function relationship may prove inadequate for some forests. Further studies are needed to assess the generality of the $b = 2/3$ relationship found here, as species-specific height–diameter relationships often deviate from it (King 1996; Thomas 1996). In particular, trees of dry tropical forests show a wide range in water use strategies (Borchert 1994) and it would be instructive to see if these forests show more variation in allometry than observed here. In conducting such studies it is important that unbiased

dimensions be used, which requires that diameters be measured above buttresses. For heights, a laser rangefinder is preferred to the traditional use of sine (viewing angle) × distance to trunk base, as the latter approach can inflate height if the vertical projection of the apparent highest point falls in front of the base (Van Pelt 2001).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Adult tree trunk diameters, heights and buckling safety factors for study species.

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