

# The role of wood density and stem support costs in the growth and mortality of tropical trees

DAVID A. KING, STUART J. DAVIES, SYLVESTER TAN\* and NUR SUPARDI MD. NOOR †

Center for Tropical Forest Science – Arnold Arboretum Asia Program, Harvard University, 22 Divinity Ave., Cambridge, MA 02138, USA, \*Sarawak Forestry Corporation, Kuching, Sarawak, Malaysia, and †Forest Management and Conservation Division, Forest Research Institute, Malaysia, Kepong, Kuala Lumpur 52109 Malaysia

## Summary

**1** The rapid growth rates of light-demanding tree species have been attributed in part to their low-density, low-cost stems. We evaluated the influence of light and biomass support costs on growth rates of trees 8–25 cm in diameter at breast height (d.b.h.) among 21 species differing in wood density in two aseasonal rain forests.

**2** Measurements of crown width, tree height, d.b.h. and wood density ( $\rho$ ) were used to estimate the stem biomass ( $M_s$ ) of a standard-sized tree (17 m tall and 16 m<sup>2</sup> in crown area), i.e. the cost in stem biomass of supporting a given sized crown at a given height.

**3** The species showed a three-fold range in support cost, which was highly correlated with wood density ( $M_s \propto \rho^{0.77}$ ,  $r^2 = 0.72$  for the log-transformed relationship). This relationship is due to the high interspecific variation in wood density and the fact that the stem diameter of the standard-sized tree increased only slightly with decreasing wood density, i.e. light-wooded species did not compensate for their lighter, weaker wood by substantially increasing stem thickness.

**4** Mean growth rate per species showed a 10-fold range and increased with the fraction of trees at least partly in gaps (gap fraction), the reciprocal of support cost ( $1/M_s$ ), and the reciprocal of wood density ( $1/\rho$ ). The relationship between mean growth rate and  $1/M_s$  was particularly strong when one outlier was excluded ( $r^2 = 0.88$ ) and among the Dipterocarpaceae ( $r^2 = 0.89$ ).

**5** Log(mortality rate), as determined for all trees per species  $\geq 1$  cm d.b.h., increased linearly with  $1/M_s$ ,  $1/\rho$  and gap fraction.

**6** These results suggest an important role for wood density and support costs in the classic tradeoff between rapid growth and increased risks of damage and death.

*Key-words:* demography, life-history strategies, mechanical support costs, tree architecture, tropical rain forest, wood density

*Journal of Ecology* (2006) **94**, 670–680  
doi: 10.1111/j.1365-2745.2006.01112.x

## Introduction

The mean growth rates of tropical tree species typically vary by 10-fold or more within any one forest (Condit *et al.* 1999; Newbery *et al.* 1999). This variation in growth has been linked to interspecific differences in crown illumination and photosynthetic capacity, and in the costs of supporting and extending the crown and protecting the leaves from herbivores and pathogens (Coley 1983; Givnish 1995; Davies 2001; Turner 2001).

These links are most apparent in the contrast between shade-tolerant species and fast-growing, gap-dependent pioneers (Swaine & Whitmore 1988; Turner 2001). There is a tradeoff between traits enhancing growth in pioneers (low-density, low-cost stems and high concentrations of nutrients in leaves associated with the proteins involved in photosynthesis) and traits enhancing survival (dense-wooded, damage-resistant stems and unpalatable leaves with low nutrient concentrations and more fibre and tannins). By enhancing the ability of pioneers to overtop competitors in gaps, the former traits further augment growth by increasing access to light.

Negative correlations between mean growth rate per species and wood density have been observed in a number of tropical forests (Enquist *et al.* 1999; Burslem & Whitmore 2003; Muller-Landau 2004). Growth rates may increase with decreasing wood density because (a) species with low-density wood tend to be less shade-tolerant and are therefore restricted to brighter-than-average microsites; (b) the thickness of the peripheral shell of stem wood corresponding to a given biomass increment is inversely proportional to wood density, so that diameter growth rates vary inversely with wood density, all else being equal; and/or (c) light-wooded species require less biomass to support their crowns, i.e. they have lower support costs, and are therefore able to achieve greater crown extension per unit of synthesized biomass, which enhances future light interception and growth.

Free-standing trees must, at a minimum, have stems that are rigid enough to prevent them from bending over under their own weight when displaced from the vertical (McMahon 1973; King 1981). Additional strength is required to resist dynamic loading by wind and falling debris, i.e. trees must have some margin of safety with respect to the above minimal design. Lower safety factors with respect to this minimum requirement have been observed in light-demanding vs. shade-tolerant species (King 1986, 1987; Rich *et al.* 1986), although not in all cases (Sterck & Bongers 1998). Light-demanding species often have low-density wood and tend to be more susceptible to breakage and uprooting (Putz *et al.* 1983). However, such differences in safety factors are due to the combined effects of differences in stem diameter and the density and mechanical properties of wood (King 1981; Niklas 1994). Thus, the translation of differences in safety factors to the biomass or energetic costs likely to influence growth is uncertain. To our knowledge, there have been no comprehensive studies of interspecific variation in support cost.

To assess the relationship between growth, support costs, wood density and light, we examined interspecific differences in these characters among 613 pole-sized trees (8–25 cm trunk diameter) of 21 species in two aseasonal Malaysian rain forests. Regression-derived allometric relationships and measured wood densities were used to estimate the stem biomass of a tree of standard height and crown area for each species. As the caloric content of wood (heat of combustion per unit biomass) is relatively constant across woody species (Smith & Tumey 1982; Philip 1994), we assumed that support costs are proportional to this standard stem biomass. Support costs, as defined here, include the construction costs of the stem, branches and structural roots, but not maintenance costs related to the nitrogen content of tissues (Givnish 1988; Ryan *et al.* 1996). However, because stems comprised 79% of the total above-ground tree biomass at one study site (Pasoh) (Kira 1978), we focused on the standard stem biomass as an indicator of support costs. The study addresses the following questions.

1. Among species, what is the relationship between stem support cost and wood density? In particular, is support cost proportional to wood density or do light-wooded species have substantially thicker stems, thereby incurring similar support costs to heavy-wooded species?
2. How does the gap association of species vary with stem support cost and wood density?
3. Are interspecific differences in growth rate related to support costs?

## Methods

### SITES AND SELECTION OF TREES

The study was carried out 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) (Davies *et al.* 2003), and Lambir Hills National Park, Sarawak, Malaysia (north-west Borneo) (4°12' N, 114°01' E) (Lee *et al.* 2002). The sites receive relatively evenly distributed rainfall, averaging 1810 mm yr<sup>-1</sup> at Pasoh and 3000 mm yr<sup>-1</sup> at Lambir (Yamakura *et al.* 1995; Noguchi *et al.* 2003). Most of the Pasoh plot is on a level alluvial plain c. 100 m above sea level (Davies *et al.* 2003), while the Lambir plot is on rugged terrain on a sandstone cuesta, ranging from 109 to 240 m above sea level (Yamakura *et al.* 1995). In both plots, all trees ≥ 1 cm in diameter at 1.3 m height have been mapped, tagged and identified, and tree diameters measured to ±1 mm at 5-year intervals (Condit 1998).

Most of the 21 chosen species were common trees that are large-statured as adults. Thus, most individuals were still juvenile in the study size range, and likely to allocate substantial biomass to stem growth rather than reproduction. The study included both light- and heavy-wooded members of the Dipterocarpaceae. At Pasoh, *Dyera costulata* was chosen as a light-wooded, non-dipterocarp emergent species, along with the pioneer species *Macaranga hypoleuca* and another of the fastest growing species, *Lithocarpus rassa* (Table 1). The fast-growing species *Adinandra dumosa*, which is strongly associated with landslips, was included at Lambir. One fast-growing, non-pioneer species, *Shorea parvifolia* (Dipterocarpaceae), was studied at both sites.

The trees analysed here had trunk diameters at breast height (d.b.h.) of 7.9–24.9 cm at the time of measurement (31 January – 15 March 2004) and, with few exceptions, were chosen from lists of trees ranging from 9 to 20 cm d.b.h. in 2000–01 at Pasoh and 8–20 cm d.b.h. in 1997 at Lambir. Typically, all such trees were measured in variable length lines of 20 × 20 m quadrats running perpendicular to the longest dimension of each plot. Trees were measured over the whole length of each plot, but slopes exceeding ~30° were mostly excluded at Lambir (18% of the plot area).

**Table 1** Characteristics of the study species. Values of diameter at breast height (d.b.h.)/tree height, crown width/tree height (ht) and diameter growth rate are species means determined from  $n = 8–25$ -cm d.b.h. trees after omitting substantially damaged or vine-laden trees, with ranges shown in parentheses for the non-normally distributed growth rates. The fraction of trees at least partly in gaps (gap fraction) is based on all trees per species and  $M_s$  is the estimated stem biomass of a standard-sized tree (17 m tall with a crown area of 16 m<sup>2</sup>). Wood densities (oven dry mass/fresh volume) were determined for trees of similar size to the study trees (number of trees sampled shown in parentheses). Large adult diameter is the 95% quantile of all diameters  $\geq 0.1 \times$  maximum diameter per species (a measure which is relatively insensitive to abundance). Large adult diameters and abundances were determined from all trees on the respective forest dynamics plot. For d.b.h./ht, crown width/ht, wood density and growth rate there were significant differences among species ( $P < 10^{-9}$ ), as determined by ANOVA of  $\log(\text{growth rate} + 1 \text{ mm yr}^{-1})$  and non-transformed values of the other three variables

| Species   | Family           | d.b.h./ht<br>(mean $\pm$ SD)<br>(cm m <sup>-1</sup> ) | Crown<br>width/ht<br>(mean $\pm$ SD) | Gap<br>fraction | $M_s$<br>(kg) | Growth<br>rate (range)<br>(mm yr <sup>-1</sup> ) | $n$ | Wood density<br>(mean $\pm$ SD) (g cm <sup>-3</sup> )<br>(sample size) | Large adult<br>diameter<br>(cm) | Abundance<br>(trees $\geq 1$ cm<br>d.b.h. ha <sup>-1</sup> ) |
|---|------------------|---|--------------------------------------|-----------------|---------------|--|-----|--|---------------------------------|--|
| Pasoh, peninsular Malaysia  |                  |   |                                      |                 |               |  |     |  |                                 |  |
| <i>Dipterocarpus cornutus</i> Dyer                                | Dipterocarpaceae | 0.786 $\pm$ 0.110                                     | 0.202 $\pm$ 0.055                    | 0.4             | 85            | 2.13 (–0.87 to 6.65)                             | 24  | 0.68 $\pm$ 0.013 (2)   | 92                              | 63.0   |
| <i>Dyera costulata</i> (Miq.) Hook. f.                            | Apocynaceae      | 1.000 $\pm$ 0.122                                     | 0.208 $\pm$ 0.085                    | 0.21            | 89            | 2.27 (–0.31 to 16.61)                            | 20  | 0.35 (1)   | 99                              | 5.1  |
| <i>Koompassia malaccensis</i> Benth.                              | Fabaceae         | 0.773 $\pm$ 0.167                                     | 0.293 $\pm$ 0.086                    | 0.59            | 80            | 2.52 (–0.58 to 5.92)                             | 28  | 0.79 $\pm$ 0.068 (4)   | 81                              | 12.7   |
| <i>Lithocarpus rassa</i> (Miq.) Rhed.                             | Fagaceae         | 0.910 $\pm$ 0.196                                     | 0.356 $\pm$ 0.110                    | 0.50            | 105           | 6.07 (2.28–17.24)                                | 17  | 0.66 $\pm$ 0.048 (3)   | 28                              | 9.9  |
| <i>Macaranga hypoleuca</i> (Reichb. f. & Zoll.) Muell. Arg.       | Euphorbiaceae    | 0.926 $\pm$ 0.229                                     | 0.309 $\pm$ 0.103                    | 1.00            | 47            | 5.43 (–0.34 to 13.08)                            | 14  | 0.32 $\pm$ 0.027 (3)   | 17                              | 2.1  |
| <i>Neobalanocarpus heimii</i> (King) Ashton                       | Dipterocarpaceae | 0.879 $\pm$ 0.131                                     | 0.341 $\pm$ 0.083                    | 0.51            | 89            | 2.43 (–0.35 to 7.75)                             | 29  | 0.69 $\pm$ 0.061 (3)   | 135                             | 63.0   |
| <i>Santiria laevigata</i> Bl.                                     | Burseraceae      | 0.874 $\pm$ 0.118                                     | 0.280 $\pm$ 0.077                    | 0.35            | 62            | 3.02 (–0.70 to 8.95)                             | 17  | 0.43 (1)   | 72                              | 10.4   |
| <i>Shorea leprosula</i> Miq.                                      | Dipterocarpaceae | 0.812 $\pm$ 0.131                                     | 0.225 $\pm$ 0.059                    | 0.77            | 41            | 5.31 (0.28–16.91)                                | 32  | 0.29 $\pm$ 0.011 (3)   | 78                              | 30.1   |
| <i>Shorea maxwelliana</i> King                                    | Dipterocarpaceae | 0.780 $\pm$ 0.119                                     | 0.286 $\pm$ 0.078                    | 0.33            | 89            | 1.38 (–0.28 to 7.68)                             | 34  | 0.79 $\pm$ 0.048 (3)   | 79                              | 116.8  |
| <i>Shorea parvifolia</i> Dyer                                     | Dipterocarpaceae | 0.850 $\pm$ 0.166                                     | 0.259 $\pm$ 0.074                    | 0.43            | 47            | 4.21 (–0.35 to 16.20)                            | 36  | 0.33 $\pm$ 0.013 (2)   | 68                              | 15.8   |
| <i>Sindora coriacea</i> (Baker) Prain                             | Fabaceae         | 0.826 $\pm$ 0.128                                     | 0.304 $\pm$ 0.064                    | 0.55            | 77            | 2.62 (–0.65 to 11.23)                            | 23  | 0.60 $\pm$ 0.002 (2)   | 86                              | 23.1   |
| Lambir Hills National Park, Sarawak, Malaysia                     |                  |   |                                      |                 |               |  |     |  |                                 |  |
| <i>Adinandra dumosa</i> Jack                                      | Theaceae         | 0.871 $\pm$ 0.161                                     | 0.251 $\pm$ 0.074                    | 0.66            | 66            | 3.67 (0.15–13.30)                                | 27  | 0.44 $\pm$ 0.040 (3)   | 33                              | 10.0   |
| <i>Alseodaphne insignis</i> Gamble                                | Lauraceae        | 0.859 $\pm$ 0.142                                     | 0.233 $\pm$ 0.039                    | 0.19            | 103           | 1.40 (0.00–3.47)                                 | 25  | 0.55 $\pm$ 0.006 (2)   | 82                              | 9.2  |
| <i>Dialium indum</i> L.   | Fabaceae         | 0.815 $\pm$ 0.100                                     | 0.281 $\pm$ 0.064                    | 0.26            | 100           | 2.27 (0.31–6.78)                                 | 27  | 0.82 $\pm$ 0.065 (2)   | 42                              | 5.3  |
| <i>Dipterocarpus globosus</i> Vesque                              | Dipterocarpaceae | 0.724 $\pm$ 0.119                                     | 0.178 $\pm$ 0.064                    | 0.23            | 88            | 0.71 (–0.30 to 3.35)                             | 37  | 0.69 $\pm$ 0.017 (3)   | 99                              | 63.8   |
| <i>Dryobalanops aromatica</i> Gaertn. f.                          | Dipterocarpaceae | 0.785 $\pm$ 0.160                                     | 0.264 $\pm$ 0.066                    | 0.46            | 85            | 2.45 (0.15–6.26)                                 | 36  | 0.72 $\pm$ 0.026 (3)   | 103                             | 202.6  |
| <i>Scaphium borneensis</i> (Merrill) Kosterm.                     | Malvaceae        | 0.777 $\pm$ 0.105                                     | 0.182 $\pm$ 0.048                    | 0.48            | 91            | 1.67 (–0.15 to 8.10)                             | 28  | 0.63 $\pm$ 0.059 (3)   | 31                              | 26.7   |
| <i>Shorea havilandii</i> Brandis                                  | Dipterocarpaceae | 0.861 $\pm$ 0.151                                     | 0.353 $\pm$ 0.105                    | 0.12            | 103           | 1.02 (–0.30 to 2.59)                             | 33  | 0.86 $\pm$ 0.065 (2)   | 58                              | 15.5   |
| <i>Shorea macroptera</i> Dyer ssp. <i>baillonii</i> (Heim) Ashton | Dipterocarpaceae | 0.870 $\pm$ 0.138                                     | 0.291 $\pm$ 0.056                    | 0.23            | 80            | 1.60 (0.15–5.92)                                 | 29  | 0.54 $\pm$ 0.081 (3)   | 44                              | 14.9   |
| <i>Shorea parvifolia</i> Dyer                                     | Dipterocarpaceae | 0.928 $\pm$ 0.147                                     | 0.296 $\pm$ 0.072                    | 0.8             | 43            | 6.08 (0.15–11.48)                                | 21  | 0.30 $\pm$ 0.075 (3)   | 97                              | 10.5   |
| <i>Swintonia schwenkii</i> Hook. f.                               | Anacardiaceae    | 0.801 $\pm$ 0.158                                     | 0.208 $\pm$ 0.059                    | 0.35            | 106           | 1.49 (0.15–4.43)                                 | 39  | 0.65 $\pm$ 0.027 (3)   | 62                              | 19.4   |
| <i>Whiteodendron moultonianum</i> (W.W. Sm.) v. Steen.            | Myrtaceae        | 0.860 $\pm$ 0.121                                     | 0.248 $\pm$ 0.052                    | 0.17            | 144           | 0.63 (–1.07 to 3.22)                             | 37  | 0.87 $\pm$ 0.032 (3)   | 41                              | 65.3   |
| Pasoh species means   |                  | 0.856   | 0.278                                | 0.51            | 74            | 3.40   |     | 0.54   |                                 |  |
| Lambir species means  |                  | 0.832   | 0.253                                | 0.36            | 92            | 2.09   |     | 0.64   |                                 |  |

## MEASUREMENTS

For each tree, we measured current diameter and the horizontally projected crown width in two perpendicular directions, including that of greatest width. Vertical height was calculated as the eye-to-tree top distance (determined by laser or optical rangefinder) multiplied by the sine of sighting angle to the horizontal (determined by clinometer) plus the vertical height from eye to tree base. Crown illumination indices were estimated using the protocol of Clark & Clark (1992), which assigns a value of 1 to crowns exposed to neither overhead nor side gaps, 2 to crowns exposed to intermediate amounts of lateral but no vertical light, 3 to crowns with 10–90% of their area exposed to vertical light, 4 to crowns with > 90% exposed to vertical light and 5 to emergent crowns for which an upward-facing cone enclosing the crown with sides angled 45° to the horizontal would include no foliage from other trees. The index was further subdivided for trees receiving lateral light only (Clark & Clark 1992; King *et al.* 2005).

Diameter growth rates were calculated as  $dD/dt = (D_j - D_i)/(T_j - T_i)$ , where  $D_j$  and  $D_i$  and  $T_j$  and  $T_i$  are, respectively, the diameters and times of measurements during the current study and the previous available census. The interval between diameter measurements ranged from 2.6 to 4 years (mean = 3.4 years) for the Pasoh study trees and 6.4–6.8 years (mean = 6.6 years) for Lambir. Mortality rates were calculated for all trees per species  $\geq 1$  cm d.b.h. as  $m = (\ln n_0 - \ln S_1)/t$ , where  $n_0$  is the number of trees in the population in 1990/1992 at Pasoh/Lambir,  $S_1$  is the number of those trees that survived until the subsequent census in 1995/1997 and  $t$  is the mean census interval for the population.

Wood densities (oven dry mass/fresh wood volume) were determined from cores taken with an increment borer from 1–4 trees per species (mean  $n = 2.6$ ) outside of the plots. The cores were taken at heights of 1–1.5 m from trees of 6.5–31 cm d.b.h., with 53/57 sample trees being within the 8–25-cm d.b.h. size range of the measured trees. Most trees were cored to depths of  $\frac{1}{3} - \frac{1}{2}$  of their diameters, and densities were determined from most or all of these core lengths, with the exception of the outermost 1 cm or so of bark and wood. The borer was angled slightly upward from the horizontal to permit drainage of sap and rainwater from the holes. Cores were placed in drinking straws in plastic bags and trimmed perpendicular to their lengths after returning from the field. Core lengths were then measured with a dial caliper and core volumes computed for cylinders of the measured length and inner diameter of the borer (0.515 cm) (Muller-Landau 2004). After drying in an oven at 67–71 °C for  $\geq 2$  days, wood densities were computed as oven dry mass/original core volume and averaged for each species.

## ANALYSIS

For each species, the fraction of study trees partly or completely in gaps was computed as the fraction of

trees with a crown illumination index  $\geq 3$ , i.e. with at least partial exposure of the crown to the sky above. This gap fraction was determined from 15–41 trees per species (mean  $n = 33.0$ ) and is equivalent to the ‘light demand’ of Poorter *et al.* (2003).

For the following allometric analyses (but not the calculation of gap fraction), trees were omitted that had any of the following: an old stem break where the above-break diameter was  $< 0.75 \times$  the below-break diameter, an estimated vine cover  $\geq$  tree leaf cover, or apparent die back of  $\geq 1/2$  of the crown or damage at the point of diameter measurement. These trees (16% of the total) sometimes had considerably below-average heights and so would have introduced additional uncertainty into the derived allometric relations. Note that mean growth rates were calculated for the less impacted study trees, while mortality rates were determined from all trees per species  $\geq 1$  cm d.b.h., as much larger samples are needed to assess the latter accurately (Condit 1998).

Trunk diameter at 1.3 m ( $D_s$ ) was estimated for trees of overall mean height ( $H_s = 17$  m) and crown area (16 m<sup>2</sup>) from species-specific multiple regressions of d.b.h. vs. (tree height + crown area). The stem biomass ( $M_s$ ) of this standard-sized tree was estimated for each species as

$$M_s = 0.5(\pi/4)\rho D_s^2 H_s \quad \text{eqn 1}$$

where  $\rho$  is wood density (oven dry mass/fresh volume) and 0.5 is the assumed form factor, defined as the ratio of stem volume to the volume of a cylinder with the height and d.b.h. of the tree. This value is similar to the mean form factor of  $0.515 \pm 0.008$  determined using the empirical stem volume equations of Fang & Bailey (1999) for 14-cm d.b.h., 17-m-tall trees (the mean dimensions of our study trees) for 23 species growing in undisturbed tropical forests on Hainan Island, China (19° N latitude). The 0.44–0.58 range (SD = 0.038) in form factor among these 23 species reflects interspecific variation in stem taper that is not included in our estimates, but this variation is small compared with the three-fold range in measured wood density that is incorporated into eqn 1. Note that because  $H_s$  and the form factor are specified, the standard stem biomass is entirely determined by the wood density and estimated trunk diameter of the standard-sized tree. However, depending on the interspecific relationship between  $D_s$  and  $\rho$ ,  $M_s$  may be correlated with one or the other of these variables, or with neither or both of them.

$M_s$  and wood density were logarithmically transformed, as this indicates the proportional relationships between variables (Niklas 1994). The gap fraction, growth rate and log(mortality rate) were related to the reciprocals of  $M_s$  and wood density, as this transformation linearized the residuals and reduced the residual standard error in all cases. Growth rate is expected to be proportional to  $1/\rho$ , all else being equal, because the

thickness of the shell of peripheral wood associated with a given stem biomass increment is inversely proportional to its density.

## Results

### GENERAL PATTERNS

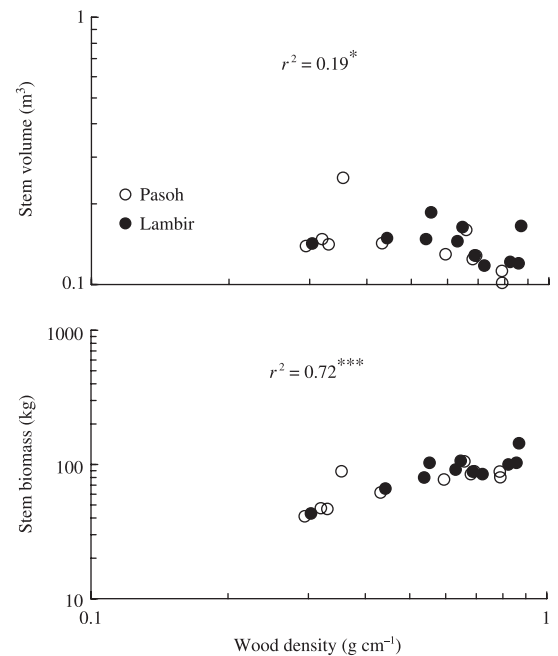
Among all trees, trunk diameter at 1.3 m height (d.b.h.) was linearly correlated with tree height over the limited size range considered here ( $r^2 = 0.53$ ). Crown width was quite variable and only weakly correlated with tree height ( $r^2 = 0.10$ ). However, the correlation between d.b.h. and crown width was somewhat stronger ( $r^2 = 0.29$ ), as wide-crowned trees tended to be thicker stemmed. Tree height and crown area accounted for 64% of the variation in d.b.h. This comparatively low correlation between d.b.h. and measures of tree size is due in part to the limited size range considered here.

### INTERSPECIFIC PATTERNS

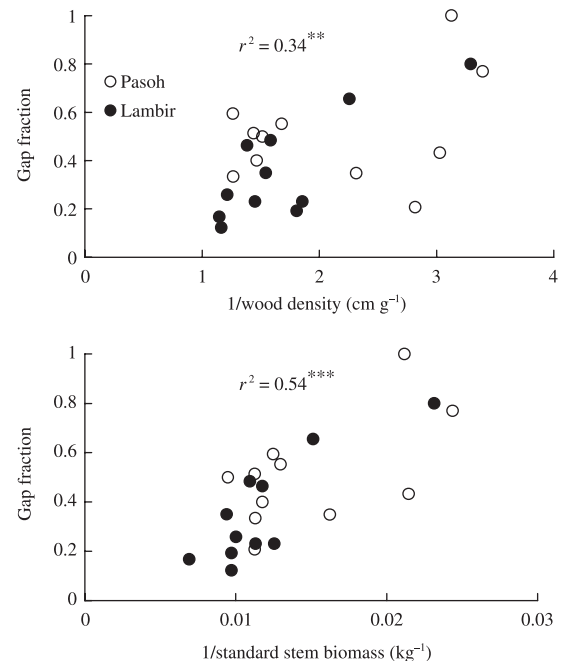
The study species varied significantly ( $P < 10^{-9}$ ) in d.b.h./tree height, crown width/tree height, growth rate and wood density (Table 1). The intraspecific variance in wood density was only 4.5% of the total, as assessed for the 14 species for which three (or in one case four) trees were sampled for density. As there were no significant site effects or interactions with site among the relationships considered, the two sites were combined in the following analyses. The one species measured at both sites (*Shorea parvifolia*) was considered separately at each site, as it showed significant differences in growth rate between the two sites. The mean ratio of crown width/tree height varied by a factor of two among species, while wood density ( $\rho$ ) varied by a factor of three (Table 1). However, crown width/tree height was not correlated with  $\rho$  ( $r^2 = 0.02$ ) nor with the fraction of trees per species that were at least partly in gaps (gap fraction) ( $r^2 = 0.04$ ).

The estimated stem biomass ( $M_s$ ) of standard-sized trees (17 m tall and 16 m<sup>2</sup> in crown area) was proportional to  $\rho^{0.77 \pm 0.11}$ , while the associated stem volume decreased slightly with  $\rho$  (Fig. 1). The gap fraction increased with both  $1/\rho$  and  $1/M_s$ , being more strongly correlated with the latter variate (Fig. 2). Note that the heaviest-wooded or heaviest-stemmed species are denoted by the left-most points on the reciprocal plots of Figs 2–4.

The mean growth rate varied among species by a factor of 10 and was most strongly correlated with the gap fraction (Fig. 3). However, with the exclusion of the one outlier, *Lithocarpus rassa* (the Pasoh species with the highest growth rate shown in Fig. 3), growth rate was most strongly correlated with  $1/M_s$  ( $r^2 = 0.88$ ), followed by gap fraction ( $r^2 = 0.74$ ) and  $1/\rho$  ( $r^2 = 0.73$ ). For the multiple regression of growth rate vs. gap

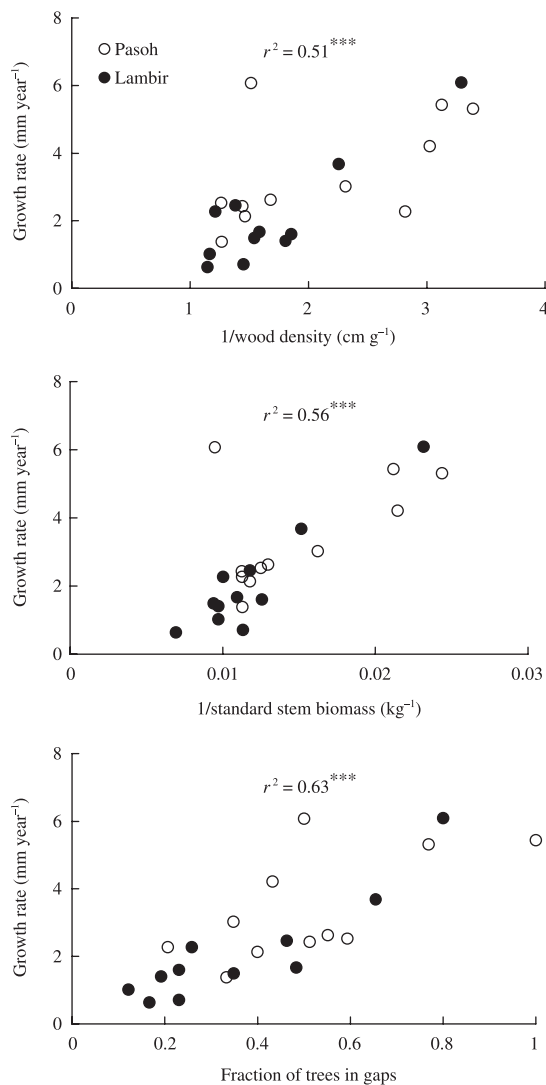


**Fig. 1** Estimated stem volume and stem biomass of a standard-sized tree (17 m tall, with a crown area of 16 m<sup>2</sup>) vs. wood density for each of the study species. \* $P < 0.05$  and \*\*\* $P < 0.001$  for logarithmically transformed variables.



**Fig. 2** Relationship between fraction of trees per species with crowns at least partly in a gap (gap fraction) vs. the reciprocals of wood density and standard stem biomass. \*\* $P < 0.01$  and \*\*\* $P < 0.001$ .

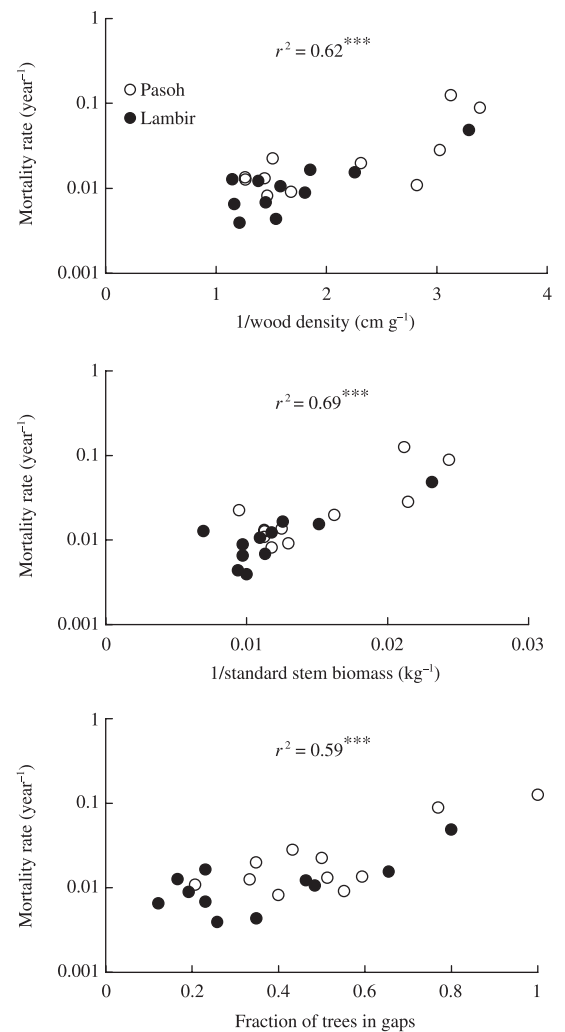
fraction +  $1/\rho$ , both slope coefficients were significantly different from zero, particularly with the exclusion of *L. rassa* (Table 2). For the regression of growth rate vs. gap fraction +  $1/M_s$ , the coefficient of the latter variable was only marginally significant ( $P = 0.07$ ), in part because the stronger correlation of gap fraction with  $1/M_s$  than with  $1/\rho$  ( $r^2 = 0.54$  vs. 0.34) increases the



**Fig. 3** Relationships between mean growth rate per species and the specified functions of wood density, standard stem biomass and gap fraction. \*\*\* $P < 0.001$  in all cases.

uncertainty regarding the separate effects of the independent variables, due to collinearity (Zar 1996). By contrast, the coefficients of both  $1/M_s$  and gap fraction were highly significant with the exclusion of *L. rassa* and for members of the Dipterocarpaceae considered alone. Furthermore, for the subset of 149 trees with the same crown illumination index ( $CI = 3$ ), mean growth rate per species was substantially correlated with both  $1/\rho$  ( $r^2 = 0.49$ ,  $P < 0.001$ ) and  $1/M_s$  ( $r^2 = 0.44$ ,  $P < 0.001$ ). In both cases the  $y$  intercept was within one standard deviation of zero, indicating that growth rate was directly proportional to either  $1/\rho$  or  $1/M_s$ . Multiple regressions involving both  $1/M_s$  and  $1/\rho$  or all three independent variables were not performed because  $\rho$  is directly incorporated in  $M_s = \rho V_s$ .

Log(mortality rate) for trees  $\geq 1$  cm d.b.h. was strongly correlated with  $1/\rho$  and gap fraction and even more strongly correlated with  $1/M_s$  ( $r^2 = 0.69$ , Fig. 4). The coefficients of gap fraction and  $1/\rho$  were both significant ( $P < 0.01$ ) in the multiple regression of



**Fig. 4** Relationships between mortality rate per species (plotted on a logarithmic scale) and the specified functions of wood density, standard stem biomass and gap fraction. Coefficients of determination are for log(mortality rate) vs. the specified variables. \*\*\* $P < 0.001$  in all cases.

log(mortality rate) against these variates, but the coefficient of gap fraction was only marginally significant ( $P = 0.06$ ) in the regression against gap fraction +  $1/M_s$  (Table 2).

## Discussion

Our results reveal large interspecific differences in diameter growth rate that were related to interspecific differences in wood density ( $\rho$ ) and standardized stem support costs ( $M_s$ ). While intraspecific variation in  $\rho$  and  $M_s$  could complicate the interpretation of these results, the observed intraspecific variance in  $\rho$  was only 1/21 of the interspecific variance. This finding is consistent with reports of weak or inconsistent relationships between intraspecific variation in  $\rho$  and growth rate among angiosperms with diffuse, porous wood (Zobel & van Buijtenen 1989; DeBell *et al.* 2001), the group including most tropical trees. By contrast, ontogenetic shifts in wood density have been observed

**Table 2** Interspecific multiple regression relationships and coefficients of determination for growth rate (Gr) and mortality rate (Mort) vs. gap fraction (gap), and reciprocals of either wood density ( $\rho$ ) or standard stem biomass ( $M_s$ ). The associated partial correlation coefficients are, respectively, the correlation of the dependent variable with the first independent variable, holding the second independent variable constant, and vice versa.  $n$  is the number of populations (= no. of species + 1)

| Relationship  | $r^2$ | Partial correlations |      | $n$ |
|---|-------|----------------------|------|-----|
| Gr = $-0.72 + 0.84^*/\rho + 4.27^{**}$ gap  | 0.72  | 0.50                 | 0.66 | 22  |
| Gr = $-1.06 + 1.08^{***}/\rho + 3.57^{***}$ gap (excluding <i>Lithocarpus rassa</i> ) | 0.92  | 0.83                 | 0.83 | 21  |
| Gr = $-1.28 + 1.13^{**}/\rho + 4.16^{**}$ gap (dipterocarps only)                     | 0.96  | 0.88                 | 0.86 | 10  |
| Gr = $-0.64 + 124^*/M_s + 3.94^*$ gap   | 0.69  | 0.40                 | 0.55 | 22  |
| Gr = $-1.32 + 215^{**}/M_s + 2.27^{**}$ gap (excluding <i>L. rassa</i> )              | 0.93  | 0.86                 | 0.64 | 21  |
| Gr = $-1.69 + 189^{**}/M_s + 3.37^{**}$ gap (dipterocarps only)                       | 0.96  | 0.88                 | 0.82 | 10  |
| Log(Mort) = $-2.66 + 0.25^{**}/\rho + 0.77^{**}$ gap                                  | 0.76  | 0.64                 | 0.61 | 22  |
| Log(Mort) = $-2.58 + 0.29^{**}/\rho + 0.54$ gap (dipterocarps only)                   | 0.91  | 0.83                 | 0.57 | 10  |
| Log(Mort) = $-2.66 + 44^*/M_s + 0.56^*$ gap   | 0.74  | 0.64                 | 0.42 | 22  |
| Log(Mort) = $-2.68 + 48^{**}/M_s + 0.44$ gap (dipterocarps only)                      | 0.91  | 0.82                 | 0.46 | 10  |

Regression slope coefficients (and associated partial correlation coefficients) significantly different from zero at \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ , (\* $P < 0.1$ ).

in light-wooded, light-demanding tropical species, which show increasing wood density with increasing distance from the central pith, i.e. the density of new wood increases as the wood-producing cambium expands outward (Wiemann & Williamson 1988, 1989; Woodcock & Shier 2002). We sought to minimize this bias by coring trees of similar size to the study trees and taking the cores used to estimate wood density over most of the distance from bark to pith. The other source of bias, variation in the standardized trunk diameter ( $D_s$ ) with light level, had a minor effect on the calculated support costs, as determined from estimates of  $D_s$  for a fixed crown illumination index of 3 (data not shown).

The strong correspondence between wood density and the estimated stem biomass of a tree of specified height and crown area (Fig. 1) therefore suggests that wood density can be used as an indicator of support costs. Because the mortality rates of trees  $\geq 1$  cm d.b.h. are largely determined by small, mostly shaded trees in wet tropical forests, such mortality rates provide a good estimate of shade tolerance, defined as the ability of a species to survive in shade (Turner 2001). Thus, the relatively strong relationships between the gap fraction and the reciprocal of wood density ( $1/\rho$ ) and between log(mortality rate) and either  $1/\rho$  or gap fraction (Figs 2 and 4) support the inferences of others that either  $\rho$  or gap fraction can be used as indicators of shade tolerance (Welden *et al.* 1991; Moorcroft *et al.* 2001; Poorter *et al.* 2003). However, there are exceptions, such as *Dyera costulata*, which has light wood, but was mostly shaded in the size range considered here and had a rather high support cost associated with its proportionately thicker stem (Table 1). The reciprocal of standard stem biomass ( $1/M_s$ ) was an even better predictor of gap fraction and log(mortality rate), implying a close correspondence between shade tolerance, typical light environment and stem support costs.

Given the above relationships, it is not surprising that mean growth rate per species is strongly correlated

with all three of gap fraction,  $1/M_s$  and  $1/\rho$  (Fig. 3). The multiple regression analyses showed growth to be related to both gap fraction and  $1/M_s$  or to gap fraction and  $1/\rho$ , depending somewhat on the species included, and the growth rates of trees of given crown illumination index showed similar correlations with either  $1/M_s$  or  $1/\rho$ . These patterns, coupled with the fact that growth is light-limited under the mean irradiances of 4–8% of full light expected for pole-sized trees (Kira 1978), support the following mechanisms. All else being equal, diameter growth rate increases with the inverse of wood density because the thickness of the shell of wood associated with a given stem biomass increment is proportional to  $1/\rho$ . However, for trees of given  $\rho$ , growth rate increases with increasing irradiance (King *et al.* 2005), which is closely related to the gap fraction. The latter trend may be enhanced by the high photosynthetic capacities of gap-associated species (Davies 1998; Turner 2001). The strong correlations between  $1/M_s$  and both  $1/\rho$  and gap fraction then result in a tight relationship between diameter growth rate and  $1/M_s$ . The strong correlation between  $1/M_s$  and gap fraction is also consistent with the hypothesis that species with low support costs are more efficient in extending their crowns, thereby attaining greater exposure to light. Projections of growth with allometric models show that height growth rates increase substantially with decreasing support costs, all else being equal (Kohyama 1991; King 2005).

By contrast, the fast-growing outlier, *Lithocarpus rassa*, suggests the involvement of other factors. The unexpectedly high growth rate of this species is probably due to the fact that its mean crown area was twice the average value for the other species and to a lesser extent to its gap fraction of 0.5, which was somewhat higher than average for species of similar  $M_s$  or  $\rho$ . This species was not an outlier in analyses of growth in relation to estimated light interception, which accounted for differences in crown area (King *et al.* 2005). Thus, variation in lateral growth may represent an alternative

strategy (King 1996), although of less importance than the wood density/support cost – shade tolerance axis, due to constraints on lateral growth by high tree densities in wet tropical forests.

The large variation in wood density, support costs and growth rate observed among the nine species of Dipterocarpaceae and five species of *Shorea* (Tables 1 & 2) indicate that substantial correlated divergence in traits can occur within limited taxonomic groups, as observed for *Acer* by Ackerly & Donoghue (1998). However, most members of the Dipterocarpaceae are canopy and emergent species, which may have diverged primarily in wood properties and other traits involved in the growth/mortality tradeoff, whereas other, less dominant families and genera may show greater divergence in adult size (Thomas 1996).

Limitations to these conclusions are that they were derived from pole-sized trees of mostly large-statured species of contrasting wood density in lowland tropical forests lacking regular dry seasons. As the shade tolerance of some species varies with ontogeny (Clark & Clark 1992; Burslem & Whitmore 2003; Poorter *et al.* 2005), different results might have been obtained for different size ranges of trees. The observed correlations might have been lower had the species been chosen at random and therefore shown somewhat less variation in wood density. By contrast, the use of measured wood densities from trees of similar size to the study trees resulted in better correlations between growth and  $1/\rho$  than those based on reported wood densities, derived mostly from mature trees (King *et al.* 2005).

For the pole-sized trees studied here, the ratio of crown width to height was unrelated to either wood density ( $\rho$ ) or gap fraction. Similarly, Poorter *et al.* (2003) found crown width to be unrelated to gap fraction (light demand) among forest trees of Africa. The occurrence of extremely wide crowns in the light-wooded neotropical and African emergent *Ceiba pentandra* (Wiemann & Williamson 1989) also supports the conclusion that wood density does not constrain crown width, given that additional strength and rigidity can readily be achieved by increasing the thickness of limbs. This pattern is consistent with the above inference that variation in lateral growth represents an independent axis of differentiation from shade tolerance and/or wood density. However, trunk diameter/tree height ratios increase with crown width/tree height, both within and among species, suggesting that stem diameter growth and crown expansion are co-ordinated to maintain stability (King 1996; Sterck *et al.* 2001), possibly by means of increased cambial growth along the parts of the trunk periphery experiencing greater stresses during tree sway (Holbrook & Putz 1989).

#### ANALYSIS OF SUPPORT COSTS

The patterns in stem biomass requirements reported here can be related to the minimum support required

by a tree subject to no stresses other than its own weight. In the absence of wind or falling debris, a tree must be sufficiently rigid to prevent itself from arcing over when its top is displaced the slightest bit from the vertical, i.e. the tree must prevent toppling due to elastic instability (McMahon 1973). The minimum basal diameter ( $d_{\min}$ ) required for stability by a vertical tree, fixed at the base with a constant ratio of crown to stem weight, approximates to

$$d_{\min} = c(g\rho_g/E)^{0.5}h^{1.5} \quad \text{eqn 2}$$

where  $g$  is the acceleration due to Earth's gravity ( $9.8 \text{ m s}^{-2}$ ),  $\rho_g$  is green (live) wood density (green wood mass including water/green volume),  $E$  is Young's modulus of elasticity for green wood,  $h$  is tree height and  $c$  is a constant that depends on stem taper and the ratio of crown to stem weight (King 1981). Given that  $E \propto \rho$ , based on wood properties for 59 tropical species reported by the US Department of Agriculture (1999) and  $\rho_g \propto \rho^{0.5}$ , derived from Suzuki (1999) for 283 Bornean rain forest species, eqn 2 implies that the minimum stem biomass ( $M_{\min}$ ) required for the standard-size tree scales as  $M_{\min} \propto \rho^{0.5}$  (see supplementary Appendix S1). This decline in minimum support cost with declining  $\rho$  occurs because a thicker and hence more stable structure can be constructed from the same wood biomass as xylem pore space is increased, an effect that is only partly offset by the weight added by partial filling of this additional pore space with water (King 1987).

The observed relationship between standard stem biomass and wood density of  $M_s \propto \rho^{0.77 \pm 0.11}$  implies that  $M_s/M_{\min} \propto \rho^{0.27}$ , i.e. there is a slight increase in the margin of safety with respect to elastic instability with increasing  $\rho$ . However, the capacity of wooden beams to resist breaking by dropped objects scales as a higher power of  $\rho$  than does  $E$  and, among tropical timbers, hardness is proportional to  $\rho^2$  (based on data from the US Department of Agriculture 1999), i.e. heavy-wooded species are substantially more impact-resistant. Thus, growth is enhanced by low support costs among light-wooded species, while heavy-wooded species should be substantially better at withstanding falling objects, chewing by herbivores (inversely related to hardness) and storm winds (Putz *et al.* 1983; King 1986; Burslem & Whitmore 2003); at Pasoh, this is also true for snapping of saplings by wild pigs (Ickes *et al.* 2003). Falling limbs and trees are a major cause of death and damage, particularly among subcanopy trees and saplings (Clark & Clark 1991; Van der Meer & Bongers 1996).

#### GROWTH AND MORTALITY TRADEOFFS

The observation that mortality rates were negatively related to standard tree support cost and wood density supports the hypothesis that there is a tradeoff between growth rate and risk of damage or death from a variety of causes, including deep shade (Kitajima 1994). Mean



wood densities of snapped trees on Barro Colorado Island, Panama, were substantially below average (Putz *et al.* 1983; Muller-Landau 2004), consistent with the above inference that species with lighter wood and lower support costs incur greater risks of breakage. Although many broken trees resprout (Putz *et al.* 1983), they suffer severe setbacks in height and their diameter growth rates may be slowed until crown area has recovered. As shade tolerance is also correlated with wood density and support cost, the leaf properties influencing shade tolerance, such as respiration rate, susceptibility to herbivores and leaf lifespan (Coley 1983; Givnish 1988; King 1994), may also affect this growth–mortality tradeoff. Photosynthetic adaptations for high productivity in high light appear to be associated with low support costs, but are also associated with higher respiration rates and reduced defences against herbivores (Coley 1983). Thus, low support costs are part of a larger suite of adaptations for rapid growth, which tend to reduce survival rates (Kitajima 1994).

The tradeoff between growth rate and mortality as influenced by support costs is augmented by additional tradeoffs between adult stature and a variety of architectural and photosynthetic characteristics (Thomas & Bazzaz 1999; Kohyama *et al.* 2003; Poorter *et al.* 2003) and between mean growth rate and the typical fertility of the soil on which a species occurs (Russo *et al.* 2005). On average, adults of small-sized species appear to be somewhat thicker-stemmed at a given height than juveniles of large-statured species (King 1996; Kohyama *et al.* 2003; Poorter *et al.* 2003). Within genera, Thomas (1996) found a negative correlation between wood density and maximum height, although this relationship was only marginally significant across common species in the Bornean rain forest studied by Kohyama *et al.* (2003). Thus, support costs may be negatively correlated with adult stature (Poorter *et al.* 2003). By contrast, our results show a 2.5-fold range in stem support cost among emergent species alone (Table 1) and small-statured pioneer species may have considerably lower support costs than shade-tolerant understorey species. Further studies are needed to evaluate the extent to which tradeoffs involving support costs are related to those involving adult stature and whether the strong inverse relation between growth and support costs found here applies across species of all sizes.

### Acknowledgements

The 52-ha Long-Term Ecological Research project at Lambir is a collaborative project of the Sarawak Forestry Corporation, Malaysia, the Center for Tropical Forest Science-Arnold Arboretum Asia Program (CTFS-AA) of the Smithsonian Tropical Research Institute and Harvard University, USA (under NSF awards DEB-9107247 and DEB-9629601 to P. S. Ashton), and Osaka City University, Japan (under Monbusho grant 06041094 to T. Yamakura, 08NP0901 to S. Tamura

and 09NP0901 to S. Sasaki). The 50-ha forest plot at Pasoh is a collaborative project of the Forest Research Institute Malaysia (FRIM), under the leadership of Dr A. Rahim Nik, CTFS-AA (under NSF award INT-84-12201 to P. S. Ashton and S. Hubbell, and grants from Conservation, Food and Health Foundation, Inc., USA, and the United Nations UNESCO-MAB nos. 217.651.5, 217.652.5, 243.027.6, 213.164.4 and UNESCO-ROSTSEA no. 243.170.6), and the National Institute for Environmental Studies, Japan. We thank FRIM and the Sarawak Forestry Corporation for permission and logistic support for D.A.K. to work in Pasoh and Lambir, respectively, Md. Zulkifli Bin Ehwan, Othman Bin Ayong, Xysctus Tan and Ahmad Bin Awang for field assistance, and Ian Baillie, Paul Moorcroft, Lourens Poorter, Sabrina Russo, G. Bruce Williamson and two anonymous reviewers for comments on the manuscript. D.A.K. was supported by a CTFS-AA fellowship and a CTFS research grant.

### References

- Ackerly, D.D. & Donoghue, M.J. (1998) Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *American Naturalist*, **152**, 767–791.
- Burslem, D. & Whitmore, T. (2003) Life history diversity and response to disturbance in a lowland tropical rain forest on Kolombangara, Solomon Islands. *Long-Term Changes in Tropical Tree Diversity: Studies from the Guiana Shield, Africa, Borneo and Melanesia* (ed. H. ter Steege), pp. 61–77. Tropenbos International, Wageningen (Tropenbos Series; 22).
- Clark, D.B. & Clark, D.A. (1991) The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology*, **79**, 447–457.
- Clark, D.A. & Clark, D.B. (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*, **62**, 315–344.
- Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209–233.
- Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P. & Foster, R.B. (1999) Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. *Philosophical Transactions of the Royal Society of London Series B*, **354**, 1739–1748.
- Condit, R. (1998) *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer-Verlag, Berlin.
- Davies, S.J. (1998) Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life history. *Ecology*, **79**, 2292–2308.
- Davies, S.J. (2001) Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology*, **82**, 920–932.
- Davies, S.J., Nur Supardi, M.N., LaFrankie, J.V. & Ashton, P.S. (2003) The trees of Pasoh forest: stand structure and floristic composition of the 50-ha forest research plot. *Pasoh: Ecology of a Lowland Rain Forest in Southeast Asia* (eds T. Okuda, N. Manokaran, Y. Matsumoto, K. Niiyama, S.C. Thomas & P.S. Ashton), pp. 35–50. Springer, Tokyo.
- DeBell, D.S., Keyes, C.R. & Gartner, B.L. (2001) Wood density of *Eucalyptus saligna* grown in Hawaiian plantations: effects of silvicultural practices and relation to growth rate. *Australian Forestry*, **54**, 106–110.

- Enquist, B.J., West, G.B., Charnov, E.L. & Brown, J.H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*, **401**, 907–911.
- Fang, Z. & Bailey, R.L. (1999) Compatible volume and taper models with coefficients for tropical species on Hainan Island in southern China. *Forest Science*, **45**, 85–100.
- Givnish, T.J. (1988) Adaptations to sun and shade: a whole plant perspective. *Australian Journal of Plant Physiology*, **15**, 63–92.
- Givnish, T.J. (1995) Plant stems: biomechanical adaptation for energy capture and influence on species distributions. *Plant Stems: Physiology and Functional Morphology* (ed. B.L. Gartner), pp. 3–49. Academic Press, San Diego.
- Holbrook, N.M. & Putz, F.E. (1989) Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (sweet gum). *American Journal of Botany*, **76**, 1740–1749.
- Ickes, K., Dewalt, S.J. & Thomas, S.C. (2003) Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology*, **91**, 222–233.
- King, D.A. (1981) Tree dimensions: maximizing the rate of height growth in dense stands. *Oecologia*, **51**, 351–356.
- King, D.A. (1986) Tree form, height growth, and susceptibility to wind damage in *Acer saccharum*. *Ecology*, **67**, 980–990.
- King, D.A. (1987) Load bearing capacity of understory tree-lets of a tropical wet forest. *Bulletin of the Torrey Botanical Club*, **114**, 419–428.
- King, D.A. (1994) Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany*, **8**, 948–957.
- King, D.A. (1996) Allometry and life history of tropical trees. *Journal of Tropical Ecology*, **12**, 25–44.
- King, D.A. (2005) Linking tree form, allocation and growth with an allometrically explicit model. *Ecological Modelling*, **185**, 77–91.
- King, D.A., Davies, S.J., Nur Supardi, M.N. & Tan, S. (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology*, **19**, 445–453.
- Kira, T. (1978) Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. *Tropical Trees as Living Systems* (eds P.B. Tomlinson & M.H. Zimmermann), pp. 561–590. Cambridge University Press, Cambridge.
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**, 419–428.
- Kohyama, T. (1991) A functional model of describing sapling growth under a tropical forest canopy. *Functional Ecology*, **5**, 83–90.
- Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T. & Kubo, T. (2003) Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *Journal of Ecology*, **91**, 797–806.
- Lee, H.S., Davies, S.J., LaFrankie, J.V., Tan, S., Yamakura, T., Itoh, A., Ohkubo, T. & Ashton, P.S. (2002) Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. *Journal of Tropical Forest Science*, **14**, 379–400.
- McMahon, T.A. (1973) Size and shape in biology. *Science*, **179**, 1201–1204.
- Moorcroft, P.R., Hurtt, G.C. & Pacala, S.W. (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–586.
- Muller-Landau, H.C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**, 20–32.
- Newbery, D.M., Kennedy, D.N., Petol, G.H., Madani, L. & Ridsdale, C.E. (1999) Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. *Philosophical Transactions of the Royal Society of London Series B*, **354**, 1763–1782.
- Niklas, K.J. (1994) *Plant Allometry: the Scaling of Form and Process*. University of Chicago Press, Chicago.
- Noguchi, S., Nik, A.R. & Tani, M. (2003) Rainfall characteristics of tropical rainforest at Pasoh Forest Preserve, Negeri Sembilan, Peninsular Malaysia. *Pasoh: Ecology of a Lowland Rain Forest in Southeast Asia* (eds T. Okuda, N. Manokaran, Y. Matsumoto, K. Niiyama, S.C. Thomas & P.S. Ashton), pp. 51–58. Springer, Tokyo.
- Philip, M.S. (1994) *Measuring Trees and Forests*, 2nd edn. CAB International, Wallingford, UK.
- Poorter, L., Bongers, F., Sterck, F.J. & Hansjörg, W. (2003) Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology*, **84**, 602–608.
- Poorter, L., Bongers, F., Sterck, F.J. & Hansjörg, W. (2005) Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. *Journal of Ecology*, **93**, 256–267.
- Putz, F.E., Coley, P.D., Lu, K., Montalvo, A. & Aiello, A. (1983) Uprooting and snapping of trees: structural determinants and ecological consequences. *Canadian Journal of Forest Research*, **13**, 1011–1020.
- Rich, P.M., Helenurm, K., Kearns, D., Morse, S.R., Palmer, M.W. & Short, L. (1986) Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest. *Bulletin of the Torrey Botanical Club*, **113**, 241–246.
- Russo, S.E., Davies, S.J., King, D.A. & Tan, S. (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology*, **93**, 879–889.
- Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J. & McMurtrie, R.E. (1996) Foliage, fine-root, woody tissue and stand respiration in relation to nutrient content. *Tree Physiology*, **16**, 333–343.
- Smith, D.W. & Tumey, P.R. (1982) Specific density and caloric value of the trunk wood of white birch, black cherry, and sugar maple and their relation to succession. *Canadian Journal of Forest Research*, **12**, 186–190.
- Sterck, F.J. & Bongers, F. (1998) Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. *American Journal of Botany*, **85**, 266–272.
- Sterck, F.J., Bongers, F. & Newbery, D.M. (2001) Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. *Plant Ecology*, **153**, 279–292.
- Suzuki, E. (1999) Diversity in specific gravity and water content of wood among Bornean tropical and rainforest trees. *Ecological Research*, **14**, 211–224.
- Swaine, M.D. & Whitmore, T.C. (1988) On the definition of ecological species groups in tropical rainforests. *Vegetatio*, **75**, 81–86.
- Thomas, S.C. (1996) Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *American Journal of Botany*, **83**, 556–566.
- Thomas, S.C. & Bazzaz, F.A. (1999) Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology*, **80**, 1607–1622.
- Turner, I.M. (2001) *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press, Cambridge.
- US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. General Technical Report 113. US Department of Agriculture Forest Service, Forest Product Laboratory, Madison, Wisconsin.
- Van der Meer, P.J. & Bongers, F. (1996) Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. *Journal of Ecology*, **84**, 19–29.

- Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, **72**, 35–50.
- Wiemann, M.C. & Williamson, G.B. (1988) Extreme radial changes in wood specific gravity in some tropical pioneers. *Wood and Fiber Science*, **20**, 344–349.
- Wiemann, M.C. & Williamson, G.B. (1989) Radial gradients in the specific gravity of wood in some tropical and temperate trees. *Forest Science*, **35**, 197–210.
- Woodcock, D.W. & Shier, A.D. (2002) Wood specific gravity and its radial variations: the many ways to make a tree. *Trees*, **16**, 437–443.
- Yamakura, T., Kanzaki, M., Itoh, A., Ohkubo, T., Ogino, K., Chai, O.K.E., Lee, H.S. & Ashton, P.S. (1995) Topography of a large-scale research plot established within a tropical rain forest at Lambir, Sarawak. *Tropics*, **5**, 41–56.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, NJ.
- Zobel, B.J. & van Buijtenen, J.P. (1989) *Wood Variation: its Causes and Control*. Springer-Verlag, Berlin.

Received 28 October 2005

revision accepted 8 December 2005

Handling Editor: Kyle Harms

### Supplementary material

The following supplementary material is available online at [www.blackwell-synergy.com](http://www.blackwell-synergy.com)

**Appendix S1** Derivation of minimum support cost