

# Illumination–size relationships of 109 coexisting tropical forest tree species

DOUGLAS SHEIL\*, AGUS SALIM\*†, JÉRÔME CHAVE‡, JEROME VANCLAY§ and WILLIAM D. HAWTHORNE¶

\*Center for International Forestry Research, PO Box 6596 JKPWB, Jakarta 10065, Indonesia, †National Centre for Epidemiology and Population Health, Australian National University, Mills Road, Acton ACT 0200, Australia, ‡Laboratoire Evolution et Diversité Biologique, UMR CNRS 5174, 118, route de Narbonne, F-31062 Toulouse, France, §School of Environmental Science and Management, Southern Cross University, PO Box 157, Lismore NSW 2480, Australia, and ¶Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK

## Summary

**1** Competition for light is a central issue in ecological questions concerning forest tree differentiation and diversity. Here, using 213 106 individual stem records derived from a national survey in Ghana, West Africa, we examine the relationship between relative crown exposure, ontogeny and phylogeny for 109 canopy species.

**2** We use a generalized linear model (GLM) framework to allow interspecific comparisons of crown exposure that control for stem-size. For each species, a multinomial response model is used to describe the probabilities of the relative canopy illumination classes as a function of stem diameter.

**3** In general, and for all larger stems, canopy-exposure increases with diameter. Five species have size-related exposure patterns that reveal local minima above 5 cm d.b.h., but only one, *Panda oleosa*, shows a local maximum at a low diameter.

**4** The pattern of species exposures at 10 cm diameter is consistent with two overlapping groups, of which the smaller (21 species, including most pioneers) is generally better exposed.

**5** Relative illumination rankings amongst species are significantly maintained over a wide range of stem sizes. Species that are well exposed at small diameters are therefore also more likely to be well exposed at larger diameters, although two species in the most exposed 25% of species at 10 cm d.b.h. drop to the lowest illumination quartile at 40 cm d.b.h., and three demonstrate the opposite (low-to-high) pattern.

**6** Species capable of achieving the largest diameters are generally recorded less frequently in shade than are smaller species, even when compared as saplings, suggesting that species achieving large mature sizes are generally shade intolerant when small. Controlling for phylogeny reveals that this relationship holds across independent lineages.

**7** We also find evidence that the range of strategies encountered is influenced by disturbance regimes.

**8** We interpret our results as indicating a continuum of strategies that reflect an evolutionary trade-off between a species' mature size and its general shade-tolerance, in combination with differentiation based on disturbance based opportunities. Species that appear similar can therefore remain ecologically distinct over their lifetimes.

*Key-words:* Allometry, canopy-position, competitive-exclusion, exposure, guilds, ontogeny, phylogenetic-regression, trade-off, rain forest, shade-tolerance.

*Journal of Ecology* (2006) **94**, 494–507  
doi: 10.1111/j.1365-2745.2006.01111.x

## Introduction

Many studies have highlighted the importance of interspecific differences in light requirement for

understanding species coexistence in tropical rain forest trees (Clark & Clark 1992; Ashton 1998; Dalling *et al.* 1998; Brown *et al.* 1999; Sterck *et al.* 2001; Turner 2001), and schemes for grouping species are often based on illumination requirements alone (Swaine & Whitmore 1988; Hawthorne 1995). Ecological theory

Correspondence: Douglas Sheil (e-mail d.sheil@cgiar.org).

has also emphasized the role of variation in the light requirements of coexisting tree species (Latham 1992; Kohyama 1993; Loehle 2000; Turner 2001; Chave *et al.* 2002). Community-scale field studies are, however, scarce: differences in shade tolerance are hard to assess because of spatial and temporal heterogeneity, and because of the large sample sizes and complex statistical procedures required.

Much of the difficulty in grasping interspecific differences in shade-tolerance lies in the ontogenic shifts that occur between tree establishment and maturity. Since larger trees tend to be better exposed, failure to account for plant size confuses any analysis of shade tolerance. We must also account for the spatial and temporal heterogeneity which affects tree establishment, growth and survival (Clark & Clark 1992; Grubb 1977; Hawthorne 1995; Parker 1995; Montgomery & Chazdon 2002).

Ability to grow and shade-out competitors varies with conditions. Partitioning of the light environment among species can promote coexistence (Latham 1992), but such partitioning remains contentious and field evaluations remain scarce (e.g. Montgomery & Chazdon 2002). Studies generally consider seedlings alone even though the logic also applies to larger trees (Sack & Grubb 2001).

Understanding how shade-tolerance may be linked with other aspects of plant biology may provide insight into species variation. Considering how variation in adult size might relate to juvenile shade-tolerance, we find arguments for null, positive, negative or mixed relationships. The null model – community wide equivalence of species with respect to shade-tolerance throughout ontogeny – follows Hubbell (2001). Evidence for these neutral models usually focuses on their ability to simulate community patterns, such as relative species abundance distributions (Chave *et al.* 2002). However, one study of tree exposure at La Selva in Costa Rica has concluded, in accord with neutral theory, that species were generally equivalent (Lieberman *et al.* 1995).

A positive relationship – increasing juvenile shade-tolerance with greater adult size – is plausible if species differentiation is primarily determined by specific successional patterns. In one of Horn's models of succession (Horn 1971), crown layering and canopy placement are the focus, but tree species replace each other in a sequence in which each subsequent species is both more shade tolerant and taller at maturity, and thus able to exclude the previous occupants. This has intuitive appeal as forest succession often presents a series of species of increasing mature stature (Sheil 2003; Falster & Westoby 2005). When diameter, rather than height, is used as a measure of size, similar patterns could result from tree architectural models in which stem-slenderness increases with shade-tolerance (Sterck *et al.* 2001).

A negative relationship – decreasing juvenile shade-tolerance with greater adult-size – is consistent with

Givnish's evaluation of tree height and resource allocation during plant growth (Givnish 1988). He argues that the largest trees must maximize energy capture in high light levels, and this will reduce juvenile shade-tolerance by comparison with small stature species. The argument begins by noting, first, that to best persist in low light, plants must maximize photon capture and minimize carbon expended. Low photosynthetic capacity is beneficial because it is less costly, but this leaves the plant poorly equipped to utilize high illumination. In contrast, plants of high-light environments benefit from high photosynthetic capacity. Second, relative metabolic costs increase with tree size, and this ultimately limits maximum dimensions. Only species with adequate resources to allocate can continue to grow and reach the largest sizes. To overcome this limit the very largest species must be very well suited to effective energy capture in the high-light environments they encounter at large sizes. Third, photosynthetic efficiency is constrained through ontogeny, i.e. a species cannot derive maximum energy from both high light as an adult and from low light while a juvenile.

Based on these points, Givnish (1988) argues that species that can become very large adult trees will be less shade-tolerant than smaller species, even as juveniles. So, there is a predicted trade-off: although taller species capture a disproportionate share of available light, they are less able to persist in low light than shorter species. We find evidence for this from Thomas & Bazzaz (1999) who examined some Malaysian species (the selection stratified by genera) and found that species capable of achieving the greater heights had lower photosynthetic efficiencies as seedlings in low light, while Poorter *et al.* (2003, 2005) found a significant positive correlation between asymptotic tree height and juvenile exposure in Liberian rain forest trees.

Various authors support the view that there might be multiple axes of size-dependent life-history differentiation (Loehle 2000; Turner 2001). Though a combination of positive (successional) and negative (old-growth) correlations of attainable-size to shade-tolerance have been indicated for one selected combination of Australian forest trees (Falster & Westoby 2005), such variation has not yet been objectively described for species rich forest communities.

When evaluating adaptive explanations for relationships between character combinations, species cannot be treated as independent because results might reflect their shared ancestral states (Grafen 1989). Such phylogenetic dependence needs to be considered in the patterns we uncover.

In this study, we examine the relationship between shade-tolerance, ontogeny and phylogeny amongst common Ghanaian canopy trees by using a large dataset and a range of analyses. We consider how crown exposure varies in relation to stem diameter, and how this varies amongst species: are there discernible groupings? We ask if the cross-species rankings of

crown exposures are maintained across sizes; how attainable tree-size relates to exposure patterns observed at smaller sizes; and whether these patterns reflect phylogeny.

## Methods

### DATA

Data derive from the Ghana National Forest Inventory Project (as discussed in Hawthorne 1995 and Hawthorne *et al.* 2001), a 0.25% systematic sample of 127 high-forest reserves in Ghana. Forest reserves have been established since the 1920s and have been subjected to various interventions (see Hawthorne & Abu-Juam 1995). Annual rainfall ranges from 1000 mm to 2250 mm. Forest zones are divided into wet, moist and dry based on rainfall and seasonality (Hawthorne 1995).

One-hectare plots were located at 3077 locations. All living trees  $\geq 30$  cm diameter were measured. Stems  $\geq 5$  cm and  $\geq 10$  cm diameter were recorded in 0.05 ha and 0.1 ha subplots, respectively (Hawthorne 1995). Stem diameters (d.b.h.) were recorded, at 1.3 m height or above any buttresses or deformations. Buttressing and fluting were not a serious concern for stems below 40 cm d.b.h. Overall, 367 251 trees were recorded, and 298 318 were identified to species. Species included in our analysis (criteria outlined below) are listed with their families, authorities and attributes in Appendix S1 (see Supplementary material). Nomenclature follows Hawthorne (1995).

Crowns of unbroken stems, free of major lianas, were classified by trained survey teams as: 4 = fully emergent (no other vegetation in an inverted vertical cone of  $45^\circ$ ), 3 = fully exposed from above (other than as 4), 2 = partly exposed to direct light, or 1 = fully over-shadowed (Hawthorne 1995; similar to Dawkins 1956, 1958, but Dawkins' classes 2 and 3 are equivalent to class 2 here). Light conditions overlap between such classes but investigations of crown scores and local estimates of irradiation made with hemispherical photography show a strong correlation (Brown *et al.* 2000). Such classes are simple to implement and can be objectively replicated (Clark & Clark 1992; Jennings *et al.* 1999).

Ghanaian forests have been disturbed by various processes both natural and man-made. We do not claim that the forests are unaffected by these disturbances: the average understorey stem may achieve slightly higher canopy illumination than would have occurred under more pristine conditions and the relative abundance of more heliophile (light demanding) species are certainly increased. We do however, assume that the crown-exposure summary for each individual species is primarily a manifestation of its relative biology and not an artefact of local disturbance histories. We are confident in asserting this due to (i) the broad area sampled (avoiding biases from specific histories), (ii) the fact that areas with low tree cover provide few trees to the analysis, and (iii) the consistency of general

results with exploratory evaluations, which exclude data from more disturbed sites.

### MULTINOMIAL MODELS

Multinomial models are a form of standard generalized linear model (GLM) (Hosmer & Lemeshow 1989; McCullagh & Nelder 1989) developed for categorical data. These models allow us to estimate ordinal response data (here, exposure classes) while controlling for an explanatory variable (here, stem diameter). *R* version 1.7.1 ([www.r-project.org](http://www.r-project.org)) was used to estimate all models in this paper. Model based summaries reduce noise and potential bias from uneven or skewed observation densities on the explanatory variable.

The standard multinomial approach is as follows. Let  $f_i(d)$  be a function of tree diameter  $d$ , and  $p_i$  be the probability for a tree to be in the exposure class  $i$  ( $i = 1$  to 4) that is defined by the relationship.

$$p_i = \exp(f_i) / (1 + \exp(f_1) + \exp(f_2) + \exp(f_3)), \text{ where } i = 1 \text{ to } 3$$

As the four probabilities add to one, the fourth class is expressed as  $p_4 = 1 - p_1 - p_2 - p_3$  (NB results are independent of the exposure class designated as analytically redundant). The function  $f_i$  defines the relationship between d.b.h and the proportion of crowns in class  $i$ . The modelled mean crown exposure  $E$ , is calculated as a function of  $d$ ,  $E = p_1 + 2p_2 + 3p_3 + 4p_4$ .  $E_d$  is our shorthand for specific calculated  $E$  values at the given value of  $d$  (d.b.h. in cm).

Our analyses include the correlation of stem exposure estimates across size-classes. We therefore developed independent models for smaller and larger stem sizes (above and below 30 cm diameter). This division ensures that correlations determined across sizes are based on independent estimates and are not influenced by non-independent parameter errors generated in model fitting.

We used the Akaike Information Criterion (AIC, Akaike 1974) to select the best-fit models. We compared models: the 'best' model has the lowest AIC value, and if two models differ by three AIC units or more the difference is significant at  $P = 0.05$  (Burnham & Anderson 1998). We fitted models of exposure class with linear, logarithmic, quadratic and cubic terms for d.b.h. The most parsimonious model (lowest AIC), for 96 out of 109 species, was  $f_i = a_i + b_i \ln(d) + c_i d$ . None of the 13 remaining species showed convincing deviation from this basic form, and it was applied to all the species to ease computation and comparison. Next, we investigated if there were discernible species-specific effects within the crown exposure–diameter relationships. To explore this we fitted two models:

$$\text{Model 1 (M1): } f_i = a_i + b_i \ln(d) + c_i d$$

$$\text{Model 2 (M2): } f_{ij} = a_{ij} + b_{ij} \ln(d) + c_{ij} d, j = 1, 2, \dots, 109$$

Where  $\ln(d)$  is the natural logarithm of stem diameter  $d$ ,  $a$ ,  $b$  and  $c$  are fitted parameters,  $i$  is (as before) the exposure class label and  $j$  is the species label.

#### MODEL DEVELOPMENT

We focused on large canopy species – species that compete directly for canopy space – so our analysis includes only species with at least one stem diameter record exceeding 80 cm and two exceeding 70 cm (though arbitrary, this avoids single erroneous readings dictating membership). We have examined our results with various population and data definitions that are not all reported below, but the consistency of these various approaches adds confidence to our results.

In model fitting, we excluded all stems over 80 cm diameter to reduce differential leverage from unequal stem densities at larger sizes. We also excluded stems of d.b.h. 20–29 cm as data for some species were too sparse. (For both cases, including the complete data gave results consistent with the more conservative results we quote below).

For our principal analyses, species with less than 200 observations were excluded. In addition, we omitted four species whose parameter estimates failed to converge in the model fitting (*Albizia ferruginea*, *Entandrophragma candollei*, *Pseudospondias microcarpa* and *Talbotiella gentii*) as no optimal model could be determined. These final analyses included 109 species, ranging from 210 records for *Chrysophyllum pruniforme* to 11 296 for *Strombosia glaucescens*. We assessed model fit using the most commonly used pseudo  $R^2$  procedure following Cox & Snell (1989). We provide these per-species results and the best fit model parameter values in Appendix S2.

We note that practitioners in fields who deal more regularly with multinomial data models suggest that 400 independent observations is a ‘rule of thumb’ for models to behave reliably (e.g. Louviere *et al.* 1999). We examined various more conservative selection criteria such as rejecting species with fewer observations than 400 and 800 (analyses of 90 and 66 species, respectively), but the results were consistent with those for the larger analyses quoted below.

The most suitable measure of species size depends on the nature of the underlying hypotheses. In our study, we are examining proposals (albeit indirectly) related to the metabolic demands experienced by trees that influence their ability to achieve large size. The ideal measure is ‘maximum size’, but sample based measures such as the ‘biggest stem’ show unacceptable sample-size dependence and are unduly influenced by single erroneous readings. We therefore used the 95th percentile ( $p_{95}$ ) diameter for all stems  $\geq 30$  cm diameter as a surrogate for maximum size ( $max-d$ ) of each species. This measure is statistically robust given our large sample sizes, and avoids additional modelling assumptions. Exploratory evaluations showed that this

measure is robust to inclusion or exclusion of disturbed areas.

#### GUILD INFORMATION

Hawthorne (1995, 1996) determined guilds, judged pragmatically on perceived shade-tolerance, including exposure patterns of regeneration (stems  $< 5$  cm d.b.h.) and observations of larger trees ( $> 20$  cm d.b.h.) for all the species examined here. Pioneers are species that are consistently well exposed, notably so as saplings, while shade-bearer species are consistently found mainly in shade. Non-pioneer light demanders (NPLDs) tend to be shaded at small diameters and illuminated when large, while cryptic pioneers show the opposite pattern. As shade tolerance is likely to be related to general wetness of forest type, we concur with Hawthorne (1993, 1995) in separating into special guilds those species generally found in open woodland (savanna species) and in wet areas (swamp species) even though they sometimes occur within closed forest.

#### ANALYSIS OF SPECIES EXPOSURE $E$

The distribution of  $E$  values amongst species is evaluated as unimodal (single peaked), bimodal (two peaked) or multimodal (three or more peaked) by fitting the best fit models involving one, two or more Normal distributions. (We know from the Central Limit Theorem that, if samples are drawn from one multinomial distribution, the mean values will follow one Normal distribution, and, similarly, multiple Normal distributions will result from samples derived from multiple multinomial distributions). To estimate parameter distributions (i.e. mean and variance) of each of the components of the Normal mixture, we use a standard maximum likelihood method (Mardia *et al.* 1979; McLachlan & Krishnan 1997). Again, our best model is determined by the lowest AIC value.

Given multiple overlapping groups, species membership is based on probabilities. Specifically, from Bayes conditional probability formula, the probability of a species with mean score  $m$  belonging to group A is proportional to (proportion of group A in general population)  $\times$  (probability that the species has mean score of  $m$ , given it belongs to group A), i.e.  $P(A | m) = P(A) \cdot P(m | A) / \text{constant}$ . In practice, we identify the boundary value(s) of  $m$ , for which group membership of A is more probable than membership of any other group and species within this range are considered members.

As  $E$  derives from an ordinal-scale, tests of association are performed with rank correlation methods (Kendall & Gibbons 1990; Zar 1996).

To weigh the evidence of specific size–exposure behaviours, such as local minima or maxima, an indicative probability statistic is calculated as one minus the proportion of 1000 bootstrapped models that exhibit such behaviour (Efron & Tibshirani 1994). The

bootstrap sample is constructed as follows: at each observed d.b.h. (per cm), we sample (with replacement) the crown exposure score. The sample size at each d.b.h. is the number of observed stems at that d.b.h. This process is repeated for every observed d.b.h. The collated sample is then used to estimate the model and, using the model parameter estimates,  $E$  is computed across d.b.h. and the existence/nonexistence of local minima/maxima is recorded. Usually  $P$ -values assess the likelihood of rejecting a 'true' null hypothesis, but here it is assumed false and we estimate the ability [power] to detect this. As with conventional probabilities, the evidence is considered strong if the value is less than 0.05, i.e. if 95% or more of bootstrapped models exhibit the behaviour. For simplicity, we refer to these measures as 'bootstrap  $P$ -values'.

To verify some of our model results, we also used a bootstrap approach to estimate mean crown exposures directly from the data (independently from our models) using all 61 species that had more than 50 individuals in both 10–15 cm and 40–45 cm diameter size classes. For each size class and each species, we calculated the exact probability  $p_i$  that one of the  $n > 50$  individuals chosen at random had a crown exposure  $i$ . Next, we calculated  $Q(E)$ , the species-specific distribution of the mean crown exposure for each diameter class, given  $n$  randomly chosen exposures  $e_k$ , that is  $1/n \sum_{k=1}^n e_k$ . This multinomial distribution was estimated numerically using a bootstrapping technique. To compare the species exposure rankings between diameter classes we calculated a Spearman's correlation index 100 times using mean crown exposures independently drawn from the distribution  $Q(E)$  and used the mean index to estimate significance (Zar 1996). Thus, we tested whether the species ranking of light exposure in the 10–15 cm class was maintained at 40–45 cm. We also analysed each forest type separately.

#### PHYLOGENETIC REGRESSION

Adaptive explanations for correlations amongst species characteristics must account for the potential influence of common ancestry (Grafen 1989). We tested for phylogenetic independence using a regression approach in which each distinct phylogenetic branch-point provides a single independent contrast against which an adaptive hypothesis can be assessed ('phylo8.glm', Grafen 1989). The phylogenetic evaluations were based on a molecular-cladistic study of genera, families and orders (revision R20030804, Webb & Donoghue 2003).

We used this regression approach to predict size ( $max-d$ ) from our modelled  $E$  estimates for selected reference diameters. As with all regression models, errors associated with the explanatory variable  $E$  are not reflected in the estimates of fit, however, for all key results, we tried swapping dependent and explanatory variables and found that these yield similar levels of significance. Log transformations of the data had negligible influence on the quoted results.

## Results

#### MODEL FITTING

For the 5–19 cm diameter range, the AIC of the all stems in the one relationship model, M1, is a significantly poorer fit than the per species model, M2 (AIC = 101237.3 vs. 55249.8,  $P << 0.001$ ). M2 is also better than M1 for the 30–80 cm interval (243934.5 vs. 284369.3,  $P << 0.001$ ). This result confirms significant variation amongst species and justifies modelling them individually (see Appendix S2 for full model details). Examples of observed and modelled mean crown exposures for two species are shown in Fig. 1. In fact, up to 60 cm d.b.h., the fit is remarkably good for all species despite the noise and over-dispersion evident in the data.

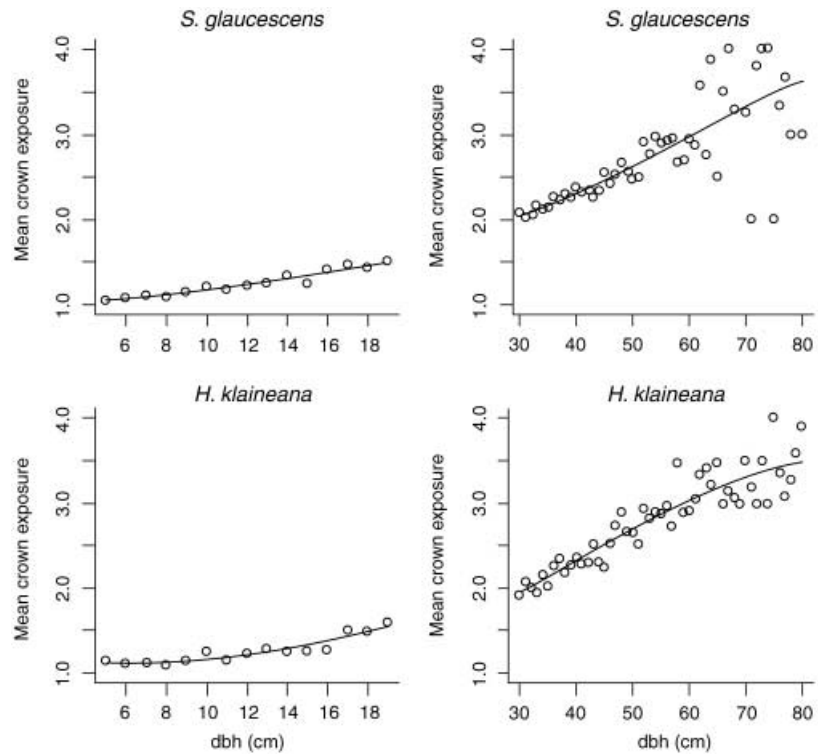
#### EXPOSURE-SIZE RELATIONSHIPS

We obtained various species-specific size-exposure relationships. Most stems are predominantly in the lowest two exposure classes, even up to stem sizes of 40 cm d.b.h., and reveal a monotonic increase in likelihood of being recorded in better-illumination as their diameter increases. We observed local minima for six species. Bootstrapped model estimates (see Methods) found these were significant only in *Nauclea diderrichii* (minimum exposure occurs at approx. 11 cm d.b.h.,  $P = 0.044$ ), and *Holoptelea grandis* (approx. at 9 cm d.b.h.,  $P = 0.008$ ). We know that these species regenerate in large-gaps or tend to be more abundant in secondary forests (Hawthorne 1996). Figure 2(a) shows that saplings of these species appear more common in more open sites than are slightly larger stems. Light-demanding species such as *Triplochiton scleroxylon* and *Terminalia superba* are more exposed than shade-tolerant species such as *Nesogordonia papaverifera* and *Dacryodes klaineana*, especially at low d.b.h. (Fig. 2c).

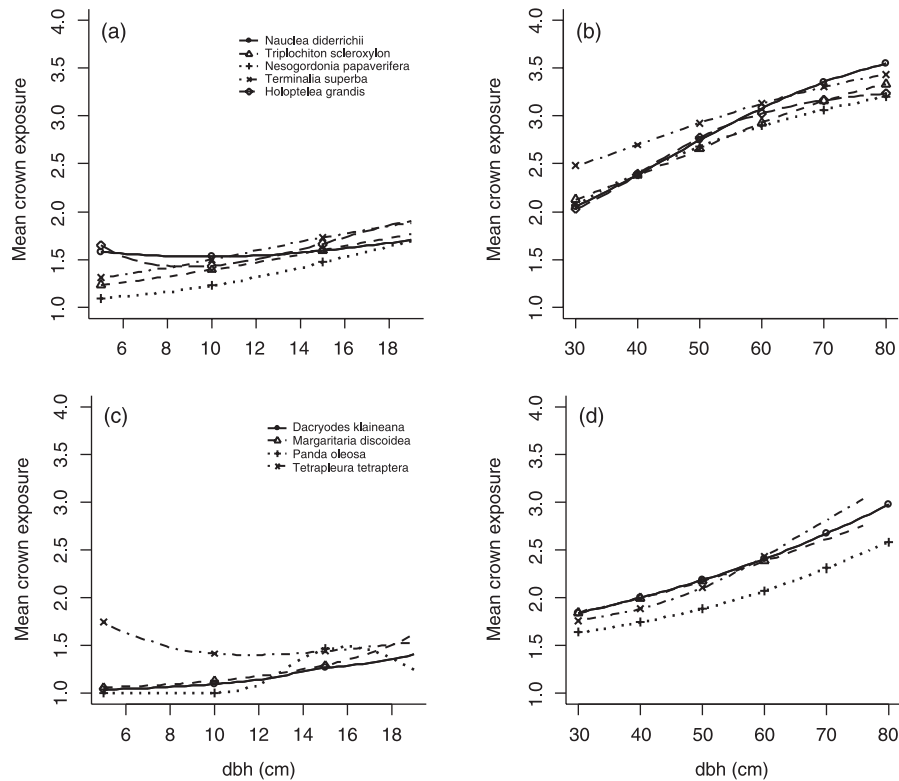
*Panda oleosa* is the only species with a local maximum at lower d.b.h. (Fig. 2c, at approximately d.b.h. = 15 cm, but note that exposure climbs with increasing diameter > 30 cm d.b.h., Fig. 2d). The bootstrap  $P$ -value for the existence of this local maximum (approach similar to that used above to investigate minima see Methods) is 0.017. The fitted model for *Lophira alata* implies a local maximum at d.b.h. = 77 cm (below  $max-d$  for this species, which is 97 cm) but the bootstrap  $P$ -value is not significant ( $P = 0.356$ ). *Carapa procera* yields a similarly non-significant pattern ( $P = 0.501$ ). Model-fits for all 109 species are shown in Fig. 3.

#### NATURAL SPECIES GROUPS

The mean  $E_{10}$  and  $E_{40}$  values, i.e. estimated mean exposures at d.b.h. 10 cm and 40 cm, respectively, differ by 1.05 units: as individual species within these two diameter classes range over 0.89 and 1.3 units, respectively, the two value sets overlap. Some species are typically as well exposed at 10 cm d.b.h. as others are at 40 cm.



**Fig. 1** Observed (circles, mean value of observation in cm interval) and modelled (line) mean crown exposures for two example species: *Strombosia glaucescens*, a species with few large diameter observations (Cox–Snell  $R^2 = 0.882$ ) and *Hannonia klaineana*, a well represented species (Cox–Snell  $R^2 = 0.811$ ). Models were not fitted from 20 to 29 cm d.b.h. as data were too sparse for several species.



**Fig. 2** Modelled exposure–diameter relationship for nine species. Left panels show the relationship at small diameter (5–20 cm), while right panels show it at large diameter (30–80 cm).

The ‘model-mean crown-exposure’ ( $E_d$ ) distribution for the 109 species appears both peaked and broadly distributed. At 10 cm d.b.h. (Fig. 4), this distribution is better described as a mixture of two normal distributions

than one (likelihood ratio test,  $P < 0.005$ ) implying a significantly bimodal distribution. Adding further Normal distributions decreases fit. Accepting this bimodal model as a basis for dividing species results in

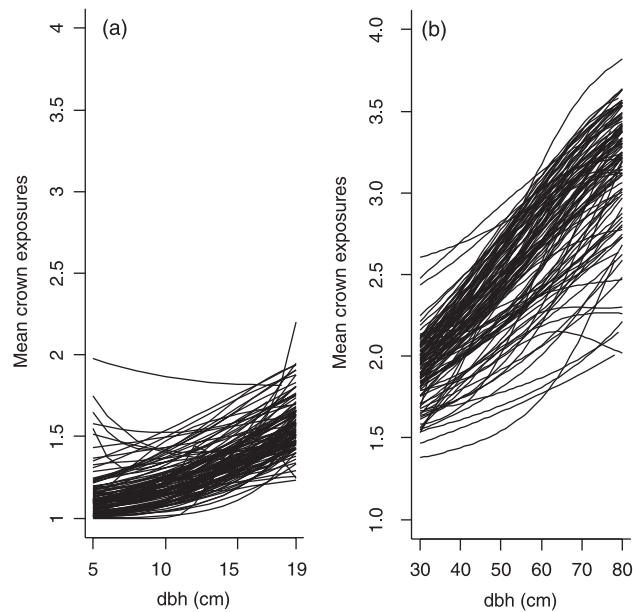


Fig. 3 The modelled mean crown exposure by diameter (d.b.h.) profiles for all 109 species.

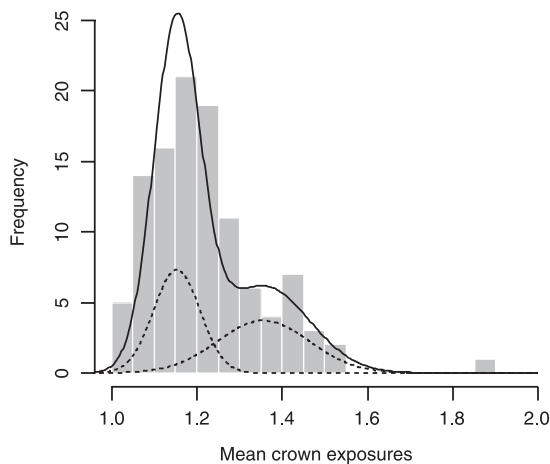


Fig. 4 Histogram of modelled mean crown exposures. The solid curve is predicted number of species in each bin, calculated using a mixture of two Normal densities (Likelihood ratio test of simple Normal density vs. mixture,  $\chi^2 = 14.12$ ,  $P < 0.005$ ). The dashed curves are unscaled densities of the two best fit Normal distributions. Based on maximum probabilities we can divide the underlying species into two groups those above and those below  $E_{10} = 1.32$ .

species being allocated to the groups to which they have the highest probability of belonging (see Methods). In our exercise, this results in all species with  $E_{10} < 1.32$  being allocated to the less-exposed group and the rest to the more-exposed group.

The more shaded group which we call *less-exposed*<sub>10</sub>, accounts for 88 of the 109 species and comprises all Hawthorne's shade-bearers and most NPLDs (39 species), but also some pioneers (10 species) and swamp species (4 species) (mean = score 1.17, SE = 0.07). The less shaded group, which we call *more-exposed*<sub>10</sub> (mean = 1.33, SE = 0.12), contains no shade-bearers, a few NPLDs (4), the majority of the pioneers (16) and one savanna species. (Note the dividing line is close to

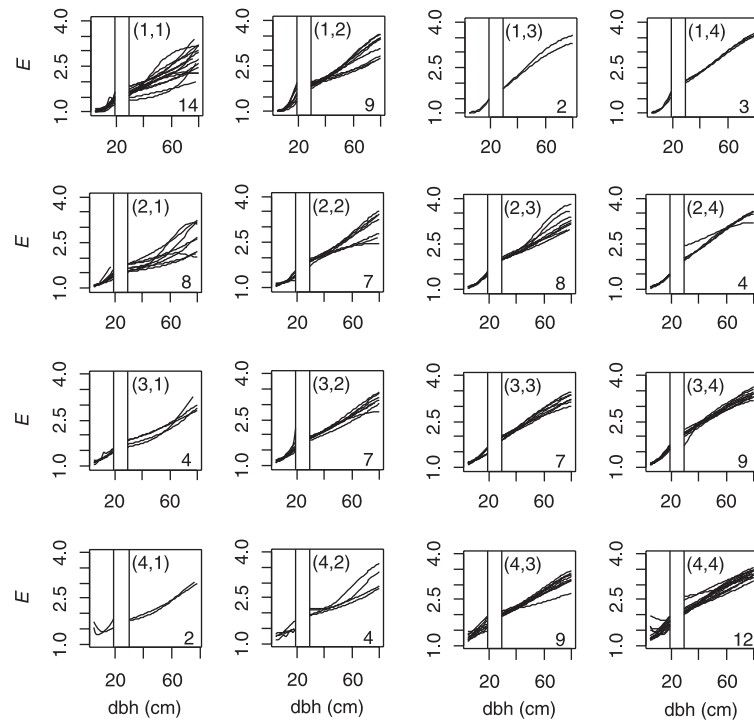
the mean of the smaller groups due to the weighted probabilities involved.)

Pioneers belonging to the second population include highly light demanding species such as *Ceiba pentandra*, *Musanga cecropioides* and *Terminalia superba*. The *more-exposed*<sub>10</sub> group is more broadly distributed and includes one high exposure outlier (*Anogeissus leiocarpa*). The two inferred groupings are differentiated by their mean exposure classes not only at  $E_{10}$  but also at  $E_{40}$  (Kruskal-Wallis test,  $P = 0.002$ , members of the *more-exposed*<sub>10</sub> remain more exposed also at 40 cm) and by their net difference in  $E$  between 10 cm and 40 cm d.b.h. ( $P = 0.025$ , *less-exposed*<sub>10</sub> members shows greater change). Though the mean *max-d* values for the *more-exposed*<sub>10</sub> group are slightly higher than the *less-exposed*<sub>10</sub> (88 vs. 84 cm) this patterns was not significant (Kruskal-Wallis test,  $P = 0.695$ ).

#### CROSS-SPECIES RANKING OF MEAN EXPOSURE

Taking all 109 species, interspecific exposure rankings remained significant across stem-sizes (Kendall's tau correlation coefficient,  $\tau$ , for 10 vs. 40 cm diameter, 0.338,  $P < 0.001$ ). If the analysis is confined to the *less-exposed*<sub>10</sub> species the correlation remains significant ( $\tau = 0.294$ ,  $P < 0.001$ ,  $n = 88$ ). If the analysis is confined to the *more-exposed*<sub>10</sub> species the correlation is positive but only marginally significant ( $\tau = 0.276$ ,  $P = 0.083$ ,  $n = 21$ ). Thus, the species more exposed at small diameters are generally the same as those that are more exposed as larger stems, both overall and within the two groups.

We confirmed this rank consistency independently of the multinomial models by bootstrapping ( $P < 0.0001$ , on 61 species with  $> 50$  individuals in both 10–15 cm and 40–45 cm classes, see Analysis). The significant



**Fig. 5** Modelled mean crown exposure,  $E$ , vs. stem diameter for species groupings based on transitions between quartiles of modelled mean crown exposures at 10 and 40 cm d.b.h. ( $E_{10}$  and  $E_{40}$ ). The horizontal axis is d.b.h. (cm) and the vertical axis is  $E$ , modelled mean crown exposure. For each group, the coordinate at the centre top is the quartile at 10 and 40 cm d.b.h., respectively (1 being the lowest and 4 the highest). The number in the bottom right corner is the number of species in the group. The region between two lines is 20–29 cm d.b.h. All species ( $n = 82$ ) in the graphs along the diagonal of the left upper corner and right lower corner follow the general vertical light trajectory in the forest canopy. The three graphs in the lower left corner (10 species) switch from high to low  $E$ , the three graphs in the upper right corner (nine species) switch from low to high  $E$ .

result persisted when data from all potentially problematic plots (disturbed, swampy, rocky) were excluded (136 743 identified trees, comprising 31 species were included,  $P < 0.005$ ). Bootstrapping by forest type reduced sample sizes and indicated significant results for the moist and the wet types (species with above 20 individuals in both 10–15 cm and 40–45 cm classes, moist: 42 species,  $P < 0.005$ ; wet: 27 species,  $P < 0.1$ , while dry forest plots provided too few observations to allow meaningful analysis).

We divided species by their exposure quartile at 10 and 40 cm d.b.h.; this division is intended only as a descriptive and heuristic approach (NB an alternative approach comparing species against a ‘mean tree’ model was considered but rejected as the prevalence of heliophile species in our sample makes the wider relevance of this per-stem reference uncertain). Forty out of 109 species had mean crown exposures at 40 cm d.b.h. in the same quartile (25% exposure group) as their 10 cm d.b.h. values (i.e. they tend to maintain their relative exposure status; Fig. 5). However, three species, *Rhodognaphalon brevicuspe*, *Irvingia gabonensis* and *Klainedoxa gabonensis*, exhibited a contrasting trend, starting in the lowest exposure quartile and ending up in the highest (Fig. 5, top right). Bootstrapping suggests that this trend is significant for *R. brevicuspe* ( $P = 0.019$ ) (i.e. 98.1% of bootstrapped curves show this pattern) but not for *I. gabonensis* or *K. gabonensis*

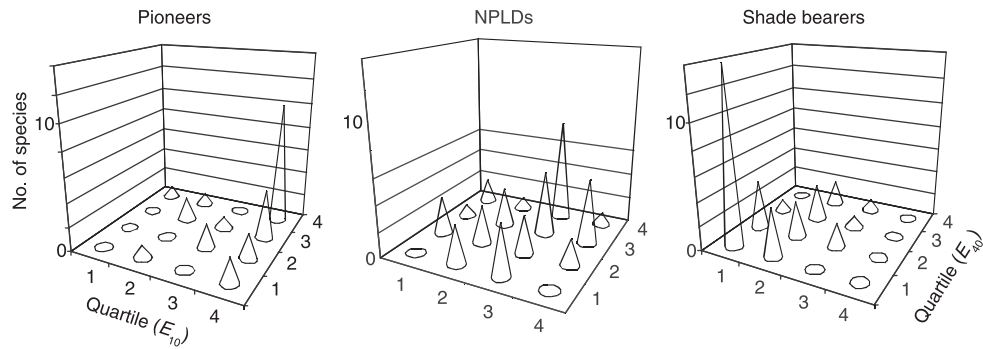
( $P = 0.348$  and  $P = 0.122$ , respectively). Two species, *Margaritaria discoidea* and *Tetrapleura tetraptera* showed the opposite trend: starting in the highest and ending in the lowest exposure quartiles (Fig. 5, bottom left; bootstrap estimates  $P = 0.088$  and  $P = 0.106$ , respectively).

The 16 transition categories (Fig. 5) had clear relationships with Hawthorne’s three principle guild categories (see Fig. 6). Pioneers predominate in the upper exposure quartile at both 10 and 40 cm d.b.h. (most clearly at 40), while shade-bearers show the opposite pattern, and NPLDs are intermediate between the two. These observations demonstrate a strong link between field experience (the basis of the guilds) and the model results.

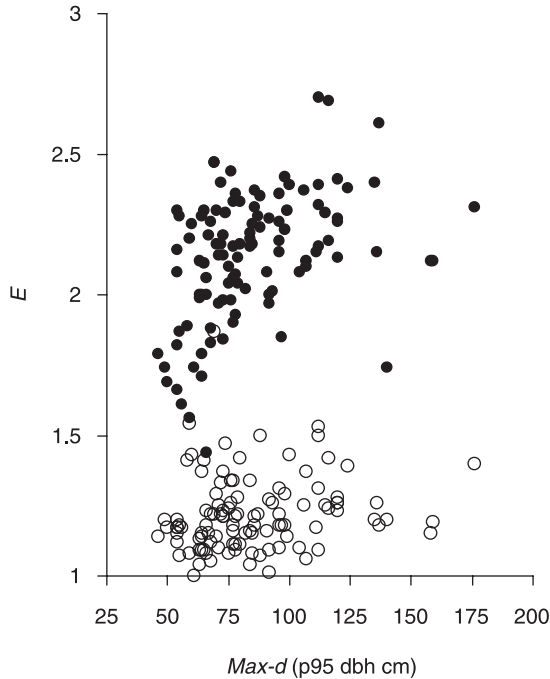
#### ULTIMATE TREE SIZE

Modelled crown exposures were positively correlated with the 95th percentile diameter ( $max-d$  for maximum diameter, which ranges from 46 cm for *Carapa procera* to 176 cm for *Ceiba pentandra*, with a per-species mean of 85 cm) of each species even at small sizes (Fig. 7, at 10 cm d.b.h.,  $\tau = 0.156$ ,  $P = 0.017$ ,  $n = 109$ , while using Pearson’s coefficient = 0.222 suggests that this relation accounts for over 20% of variance in exposure). This pattern held within the *less-exposed*<sub>10</sub> group (at 40 cm  $\tau = 0.336$ ,  $P < 0.001$ , at 10 cm,  $\tau = 0.212$ ,  $P = 0.004$





**Fig. 6** The distribution of the species by the main Hawthorne guild and by the quartiles in which their exposures are modelled at 10 and 40 cm d.b.h. ( $E_{10}$  and  $E_{40}$ ).



**Fig. 7** Modelled exposure,  $E$ , at 10 cm ( $E_{10}$ , open circles) and 40 cm d.b.h. ( $E_{40}$ , closed circles) for 109 species vs.  $Max-d$  (p95 d.b.h. of the per-species sample tree population with stems over 30 cm d.b.h.).

$n = 88$ ). For the *more-exposed*<sub>10</sub> group, the correlations though positive were significant only at large size ( $\tau = 0.024$ ,  $P = 0.880$  at 10 cm and  $\tau = 0.320$ ,  $P = 0.043$  at 40 cm,  $n = 21$ ).

As might be expected, the species that showed the biggest changes in mean exposure with size (between 10 and 40 cm d.b.h.) were also those that reached the largest sizes ( $\tau = 0.291$ ,  $P < 0.001$ ,  $n = 109$ ).

#### PHYLOGENY

Regression that partitions variation by phylogenetically independent contrasts (see Methods), using 166 branch points shows that the *max-d* vs.  $E$  relationship is positive and significant across the phylogeny (i.e. at d.b.h. = 10 cm,  $P = 0.026$ , and d.b.h. = 40 cm,  $P = 0.0001$ ). This relationship varied slightly amongst

the major clades (Asterids, Rosids, Magnoliids, in descending order of slope), but this trend was not significant ( $P = 0.27$ ). We concluded that the size-exposure relation has evolved repeatedly and independently in distinct taxonomic lineages reflecting an adaptive process.

#### CLIMATIC GRADIENT

Species are unevenly distributed across the climatic gradient and as our results may be influenced by these large-scale patterns, we conducted some exploratory evaluations. We found that trees are fractionally more exposed in the dry zone than in the wet zone, but these differences were not significant (e.g. for all sufficiently represented species between 10 and 15 cm d in the dry zone (27 species, 1751 trees) and in the combined moist and wet zones (60 species, 6534 trees), the absolute difference in illumination is 0.12, while the standard deviation of the difference was 0.14,  $t$ -value = 0.857,  $P = 0.391$ ).

We found also that the biggest trees per-plot from drier forest achieved slightly greater size on average than those in wetter forest (we estimated the 95th percentile [p95] for diameter in each plot, using all trees  $\geq 30$  d.b.h. regardless of species from plots with  $\geq 25$  such trees; the mean per-plot p95 values for wet, moist and dry are  $51.29 \pm 0.31$ ,  $52.54 \pm 0.23$ , and  $54.06 \pm 0.28$ , with  $n = 193$ , 741 and 380 plots, all contrasts significant,  $P < 0.05$ ). However, the species-specific differences appear complex. Eight of the 20 widely distributed species had significant differences in crown exposure between the dry and wetter forests (i.e. absolute difference in exposure between the two zones is larger than the sum of the standard deviation in the two zones). Five of these were more exposed in the dry zone (e.g. *Ricinodendron heudelotii*) and three in the wetter forest (e.g. *Piptadeniastrum africanum*).

#### Discussion

##### THE APPROACH

The data shows that individual subcanopy sized trees of any species occur in a wide range of illumination

conditions. The strength of our modelling lies in the ability to summarize broad population level patterns from these data.

Our multinomial models express relative crown-exposure class probabilities as a function of stem diameter for 109 canopy species. Combining these probabilities into per-species crown-illumination indices (for a nominal diameter,  $d$ ),  $E_{ds}$ , we were able to examine interspecific variation in crown exposure. Can we relate this to competition? Our understanding of plant competition is limited by our knowledge of the processes controlling individual growth (Berntson & Wayne 2000). However, we know that competing plants diminish each others' light interception not through subtle physiological processes, but rather by placing their leaves and canopy above each other (Schwinning & Weiner 1998). As  $E$  assesses crown placement directly it is a plausible index of relative competition in the stand context.

As species are not evenly distributed, environmental gradients may influence our results. In wet areas, dry forest species often thrive primarily on crests or rocky outcrops, where the vegetation is more open (see Hall & Swaine 1981; Hawthorne 1996) but this does not necessarily lead to a predictable outcome as those same dry forest species also occur exposed in dry forest. Interestingly, some species like *Khaya ivorensis*, usually fully exposed from the sapling-stage onwards in wetter areas, are more reclusive in dry areas, persisting in much smaller gaps (Hawthorne 1996). Our exploratory evaluations do not identify dominant patterns across rainfall zones: this deserves additional study.

#### VERIFICATION AND CROSS-STUDY CHECKS

Various model results were verified by bootstrapping, showing they are not artefacts of our modelling approach. Concerns over other types of artefacts are reduced through comparisons with independent results from other studies – our results are consistent with what we know of the species under consideration. For example, the patterns seen in Fig. 6 show that the Hawthorne guilds have a clear, if imperfect, association with the quartile-to-quartile exposure transition groups. General agreement is also apparent with various specific studies, for example those studies showing that seedlings of *Ceiba pentandra*, *Mansonia altissima*, *Ricinodendron heudelotii* and *Sterculia rhinopetala* (species consistently well exposed at small sizes in our models) cannot persist in typical forest shade (2% irradiance) (Swaine *et al.* 1997; Agyeman *et al.* 1999).

Comparing our results with Poorter *et al.*'s (2003) study of Liberian forest tree species is especially helpful. Our studies include 11 species in common and our approaches are complementary: we have many more records, while they included measurements of stem height and crown dimensions, and consider only old-growth forest. A cross-tabulation of the main species-specific estimates reported in both studies finds them to be in general agreement. The Liberian measurements

of maximum height (95% percentile) are highly rank correlated with our  $Max-d$  ( $P = 0.012$ ,  $n = 11$ ) and our  $E_{40}$  ( $P = 0.006$ ).  $E_{40}$  is also significantly rank correlated with the Liberian measure of light demand (percentage of trees in high light between 10 and 20 cm d.b.h.,  $P = 0.005$ ), tree height<sub>15</sub> (tree specific regressions for a tree of d.b.h. 15 cm,  $P = 0.036$ ) and marginally related to the inverse of crown depth<sub>15</sub> ( $P = 0.05$ ; all other correlations are non-significant but are signed in a manner consistent with Poorter *et al.*'s own analyses). These cross-checks bolster confidence in our results and imply wider geographical validity.

#### PATTERNS OF SPECIES VARIATION

One explanation for different species illumination profiles is differing height-diameter relationships (e.g. King 1996; Thomas 1996a; Bongers & Sterck 1998; Hawthorne *et al.* 2001). Hawthorne *et al.* (2001) and Poorter *et al.* (2003) have found that taller West African tree species are generally more slender and that this pattern is sometimes already apparent in juvenile trees (10 cm d.b.h). However, in our study the range of per-species mean  $E_{10}$  values spans nearly one full exposure class (from 1 to nearly 1.9), equivalent in magnitude to the mean per-species differences found between stems of 10 and 40 cm d.b.h. (1.2–2.1). Indeed, the  $E_{10}$  values of some species are higher than the  $E_{40}$  values of others. Even allowing for sample noise these exposure differences are unlikely to arise from interspecific height variation alone. Though clearly important, height is at best a partial answer for the variation in  $E$  values observed at small diameters.

The distribution of  $E_{10}$  values (Fig. 4) is consistent with two overlapping groups of species with 88 species in the *less-exposed*<sub>10</sub> groups and 21 in the more broadly distributed *more-exposed*<sub>10</sub> group. This result can be reconciled with the conflicting expectations of both a simple 'pioneer'–'non-pioneer' division (Swaine & Whitmore 1988) and a more general continuum (e.g. Agyeman *et al.* 1999; Montgomery & Chazdon 2002). It may indeed reflect both a division in terms of gap-dependent vs. non-gap dependent germination (as Swaine & Whitmore 1988), and a spectrum of tolerances within each group.

Germination under different light conditions has been assessed by Kyereh *et al.* (1999) for fresh seeds from 14 of our species. Only two (*Musanga cecropioides* and *Nauclea diderrichii*) showed a clear photoblastic response (a difference between light and dark): both are placed in our *more-exposed*<sub>10</sub> grouping. *Nauclea diderrichii* was also the only species tested that revealed a response to simulated low red : far-red ratio at 5% irradiance (germination was reduced by nearly 60%). Six further species (*Ceiba pentandra*, *Entandrophragma utile*, *Mansonia altissima*, *Ricinodendron heudelotii*, *Terminalia ivorensis* and *Terminalia superba*) are in our *more-exposed*<sub>10</sub> group and five (*Guarea cedrata*, *Khaya ivorensis*, *Lovoa trichilioides*, *Pterygota macrocarpa* and

*Sterculia rhinopetala*) are in our *less-exposed*<sub>10</sub> group. While the difference in the ultimate proportion of germinated seeds was not affected, the mean number of days to germinate was influenced by illumination level in five of the six species in our *more-exposed*<sub>10</sub> group (all but *Terminalia ivorensis*) but in only one (*Khaya ivorensis*) of the *less-exposed*<sub>10</sub> group. This pattern is close to significant (Fishers exact test,  $P = 0.08$ ). In any case, factors such as temperature and humidity may also contribute, alone or in combination, to gap-dependent germination.

Our models show a range of specific patterns. Local minima seen for *Nauclea diderrichii* and *Holoptelea grandis* are consistent with the fact that these species regenerate in large-gaps and tend to be more abundant in secondary forests which close up several years after initial tree establishment (Hawthorne 1996). Clark & Clark (1992) and Sterck *et al.* (1999), working in Costa-Rica and Borneo, respectively, have observed that tree species that establish in larger gaps often have lower exposure at larger sizes because they are overgrown by the rest of the gap vegetation. Similarly, our results for *Lophira alata* and *Carapa procera* (species which commonly mature in re-growth) suggest an exposure maximum may be reached at intermediate size.

*Panda oleosa* is the only species with a local exposure maximum at lower d.b.h. (Fig. 2c). We cannot identify an artefact in this result: *P. oleosa* is well recorded with 1347 observations, is distinctive and readily identified. The architecture of this elephant-dispersed species involves a highly programmed plagiotropic branching form with branches as quasi-compound leaves like *Phyllanthus*, Cook's Model (Hallé *et al.* 1978). This *E* pattern suggests that, following establishment and rapid initial growth, *P. oleosa* pauses, no-longer keeping pace with the surrounding regrowth. This may indicate either a strategy where the species reaches a size where investment in reproduction reduces growth or a specific benefit of gaining adequate size quickly (perhaps to resist larger terrestrial herbivores).

Three species, *Rhodognaphalon brevicuspe*, *Irvingia gabonensis* and *Klainedoxa gabonensis*, are in the lowest exposure quartile at 10 cm d.b.h. and in the highest at 40 cm d.b.h. This trend is significant for *R. brevicuspe*. Two species, *Margaritaria discoidea* and *Tetrapleura tetraptera* reveal the opposite trend: starting in the highest and ending in the lowest exposure quartiles. These two species also had local minima. Moving from high to low illumination with development is what Hawthorne (1996) called 'cryptic pioneers'. Such species readily persist as shade tolerant adults, despite their juvenile exposure.

#### DISTURBANCE AND SUCCESSION

Sizes achieved by the larger dominant species do increase as a relatively predictable successional pattern in some African forests (cf. Sheil 2003 for Uganda), and there is evidence in other parts of the world that shorter colonizing species pre-empt sites following disturbance

(Falster & Westoby 2005; but see Davies *et al.* 1998). Even though our results show evidence of gap dependence, they do not support a hypothesis that tree size and shade-tolerance are positively related through successional sorting. Why is this? It may be that such a relationship exists for only a subset of our species and, if so, the pattern is lost amongst the rest. The abundance of 'large-pioneers' in the West African rain forests (Turner 2001) is one factor. In addition, the fact that smaller understorey species typically establish throughout succession, and that disturbance regimes are variable in time and space provide additional complications. Established trees can benefit from the improved illumination resulting from a local tree-fall event or similar without this involving a successional component of composition change. While the relevance of successional sorting for non-pioneer species remains debated (Sheil & Burslem 2003), the importance of variation in responses to different disturbance regimes (and disturbance events) by trees of different sizes and types is increasingly highlighted (Kohyama 1993; Loehle 2000; Turner 2001). The range and variety of size-exposure relationships in Ghanaian forest trees appears to reflect both size-related gradients and disturbance.

#### TRADE-OFFS

Our results show that, amongst 109 common forest tree species, relative illumination rankings are significantly (but imperfectly) maintained over a wide range of stem sizes. The positive rank correlation between *max-d* and exposure at small diameters is especially striking. This implies that juveniles of larger species are typically more exposed (less shade-tolerant) than those of typical small-tree species of similar diameter. These patterns are robust to a broad range of analytical choices. Even though many species may be very similar (as seen in the tight grouping of species within Fig. 3) our detection of structure in the variation shows that coexisting tree species are not equivalent through ontogeny. Of course, with many coexisting species, the mean differences between the most similar species are small – but it would be a mistake to assume that such variation is irrelevant. Species need not be especially different to remain ecologically distinct over their lifetimes.

Plant characteristics associated with shade-tolerance are not evenly distributed amongst higher taxa (Bazzaz 1990). Nonetheless, our phylogenetic analyses indicate a significant pattern of correlation between attainable size and juvenile shade-tolerance independent of phylogeny, suggesting a common adaptive process.

Canopy trees have evolved the ability to reach large size because this is favoured by competition for light, but size is ultimately limited when the marginal advantages of even larger sizes are outweighed by the added costs (Iwasa *et al.* 1984). As tree size increases, respiration and maintenance requires an increasingly large proportion of the plant's energy. At very large sizes,

only the most photosynthetically efficient trees have enough spare carbon to allocate to additional growth as well as to maintenance (Givnish 1988) and reproduction (Coley & Barone 1996). Our results show that in Ghana the tallest species do indeed appear less likely to persist in shade as juveniles than are smaller species. So does this represent a trade-off?

Outside of early successional environments, taller plant species in various habitats *are* typically found to be better suited to efficient energy capture at high light and smaller species at lower light (Field & Mooney 1986; Hirose & Werger 1987; Thomas & Bazzaz 1999; Anten & Hirose 2003) and various arguments and studies imply that these adaptations are somewhat constrained through ontogeny (see Givnish 1988, 2002). Given these generalities, some trade-off – or at least an upper boundary presented by a trade-off – seems inevitable (Givnish 1988, 1995; Westoby *et al.* 2002). This then poses the alternate question: why, if it reflects a real biological limit, is it not more visible? Even in our Ghanaian data the relationship (juveniles of larger species being less shade-tolerant) is not especially strong. Why for example, do Aiba & Kohyama (1997) not detect a negative relationship between species maximum size and juvenile crown exposure among 14 non-pioneer species coexisting in their study in Japan?

One factor accounting for variation in community-wide size trade-off patterns is likely to be ontogenic plasticity. In our phylogenetic analyses, we noted the range of slopes (size vs. juvenile exposure) amongst major plant groups. We also noted that two of only three species which start in the lowest illumination  $E_{10}$  quartile and end in the highest  $E_{40}$  quartile are in the Irvingiaceae, suggesting distinctive ontogenic plasticity in this family. Taxonomic factors appear influential.

A more general explanation for differences amongst communities lies in the costs and benefits of adult tree size under real conditions. We already noted that species will evolve to be bigger only while the advantages of additional size are not outweighed by their costs. Tree size has various costs in addition to energetic demands (Smith & Huston 1989; Westoby *et al.* 2002). Such costs will vary with location. For example, taller plants suffer greater desiccation load, while understorey plants stay cooler and can keep respiring for longer in drier conditions (Schwinning & Weiner 1998). In rain forests struck by extreme droughts, large-stems may suffer higher relative mortality than small stems (e.g. van Nieuwstadt & Sheil 2005). Indeed various disturbance processes show size-selective effects: for example wind storms generally impact forests while taking a greater toll of larger than smaller stems (e.g. Ostertag *et al.* 2005). More generally, as the likelihood of dying before reaching reproductive age increases, long-term (large-sized) strategies are less favoured (Makela 1985; Thomas 1996b; Kohyama *et al.* 2003). Various theoretical studies also show that tree size can evolve as determined not only by direct competition amongst stems but also by other more intermittent

threats and opportunities (e.g. Kohyama 1993; Benton & Grant 1999; Iwasa 2000). Drawing these ideas together we predict that the apparency of a species maximum size vs. juvenile shade tolerance trade-off will vary across tree communities according to the evolutionary context and the community history regarding how the costs and benefits of tree size have played out. A trade-off is likely to be more apparent in communities where factors that interact with tree-size and tree persistence (such as drought, strong winds and disturbance regimes generally) have had little relative influence.

#### ILLUMINATION CHANGE AND LIFE-HISTORY ROULETTE

The range of  $E$  values across all stem sizes implies that minor changes in illumination (small scale canopy disturbances or increasing canopy closure) will influence different species to different extents. If different species are sufficiently favoured at different times and places, this will promote diversity (Latham 1992; Montgomery & Chazdon 2002). Such a process might be viewed as each species being required to make a sequential series of constrained bets on the best illumination conditions to be adapted for at any moment (where all betters have some chance of winning) and where the overall spread of bets are adopted according to their likelihoods and the choice of other players. Local-scale outcomes are largely stochastic, but the overall diversity of environments and their spatial and temporal dimensions provide opportunities for which different species, and individuals, are more or less suited. These opportunities, and the ecological and evolutionary interplay among the strategies that benefit from them, appear crucial to understanding the processes that govern tree community richness. Our study shows that aspects of such variation can potentially be described from suitable large scale inventory data.

#### Conclusions

Crown exposure records can help differentiate shade-tolerance attributes of species. The realization that tree species have different and dynamic shade-tolerances and adaptations as they develop has considerable significance for our understanding of species life history, tree diversity and coexistence, as well as for forest management. Employing data from a large forest inventory, we have inferred functional trade-offs and disturbance dependence from a static demographic study. Species that can achieve the largest sizes typically have lower shade tolerance than juveniles of smaller taxa. This apparent trade-off appears consistent across phyla, though there are various interesting exceptions. These patterns appear adaptive relating to tree size, ontogeny and disturbance. Identifying and describing such relationships will help achieve a more realistic, species-centred understanding of species variation, persistence and community dynamics.

## Acknowledgements

We thank David Burslem, Laura Snook, Robert Nasi, Erik Meijaard, Tony Cunningham, Jeremy Midgley, Lourens Poorter, Frans Bongers, Sean Thomas, Deborah Clark, Frank Sterck, S. Aiba and anonymous referees for comments on earlier manuscripts. Alan Grafen kindly provided advice on the phylogenetic analysis. Data was generously made available by the Ghanaian Forest Department. See Hawthorne (1995) for fuller acknowledgements for the data set, a combination of many people's efforts. Preparation of the paper was made easier by Indah Susilanasari and the CIFOR library staff.

## References

- Agyeman, V.K., Swaine, M.D. & Thompson, J. (1999) Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology*, **87**, 815–827.
- Aiba, S. & Kohyama, T. (1997) Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. *Journal of Ecology*, **85**, 611–624.
- Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transaction on Automatic Control*, **19**, 716–723.
- Anten, N.P.R. & Hirose, T. (2003) Shoot structure, leaf physiology, and daily carbon gain of plant species in a tallgrass meadow. *Ecology*, **84**, 955–968.
- Ashton, P.S. (1998) Niche specificity among tropical trees: A question of scales. *Dynamics of Tropical Communities* (eds D.M. Newbery, H.H.T. Prins & N.D. Brown), pp. 491–514. Blackwell Science, Oxford, UK.
- Bazzaz, F.A. (1990) Successional environments: plant–plant interactions. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 239–263. Academic Press Inc, San Diego, USA.
- Benton, T.G. & Grant, A. (1999) Optimal reproductive effort in stochastic density-dependent environments. *Evolution*, **53**, 677–688.
- Berntson, G.M. & Wayne, P.M. (2000) Characterising the size dependence of resource acquisition within crowded plant populations. *Ecology*, **81**, 1072–1085.
- Bongers, F. & Sterck, F.J. (1998) Architecture and development of rainforest trees: responses to light variation. *Dynamics of Tropical Communities* (eds D.M. Newbery, H.H.T. Prins & N. Brown), pp. 125–162. Blackwell Science, Oxford, UK.
- Brown, N., Jennings, S., Wheeler, P. & Nabe-Nielsen, J. (2000) An improved method for the rapid assessment of forest understorey light environments. *Journal of Applied Ecology*, **37**, 1044–1053.
- Brown, N., Press, M. & Bebbler, D. (1999) Growth and survivorship of dipterocarp seedlings: differences in shade persistence create a special case of dispersal limitation. *Philosophical Transactions of the Royal Society London, Series B*, **354**, 1847–1855.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference*. Springer, New York.
- Chave, J., Muller-Landau, H.C. & Levin, S. (2002) Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist*, **159**, 1–23.
- Clark, D.A. & Clark, D.B. (1992) Life history diversity of tropical trees. *Ecological Monograph*, **62**, 315–344.
- Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defences in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305–335.
- Cox, D.R. & Snell, E.J. (1989) *Analysis of Binary Data*, 2nd edn. Chapman & Hall, London.
- Dalling, J.W., Hubbell, S.P. & Silvera, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Tropical Ecology*, **86**, 674–689.
- Davies, S.J., Palmiotto, P.A., Ashton, P.S., Lee, S.A. & Lafrankie, J.V. (1998) Comparative ecology of 11 sympatric species of *Macaranga*. Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology*, **86**, 662–673.
- Dawkins, H.C. (1956) *Crown Classification of Natural Forest Trees*. Uganda Forest Department Technical Note, No. 17/56.
- Dawkins, H.C. (1958) *The Management of Natural Tropical High-Forest with Reference to Uganda*. Paper No. 34, Commonwealth Forestry Institute, Oxford, UK.
- Efron, B. & Tibshirani, R. (1994) *An Introduction to the Bootstrap*. CRC press, London, UK.
- Falster, D.S. & Westoby, M. (2005) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology*, **93**, 521–535.
- Field, C. & Mooney, H.A. (1986) The photosynthesis–nitrogen relationship in wild plants. *On the Economy of Plant Form and Function* (ed. T. Givnish), pp. 25–55. Cambridge University Press, London, UK.
- Givnish, T.J. (1988) Adaptation 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. Chapman & Hall, New York, USA.
- Givnish, T.J. (2002) Ecological constraints on the evolution of plasticity in plants. *Evolutionary Ecology*, **16**, 213–242.
- Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society of London*, **205**, 581–598 and <http://users.ox.ac.uk/~grafen/phylo/index.html>.
- Grubb, P.J. (1977) The maintenance of species richness in plant communities. The importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- Hall, J.B. & Swaine, M.D. (1981) *Distribution and Ecology of Plants in Tropical Rain Forest*. Junk Publishers, The Hague, Netherlands.
- Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) *Tropical Trees and Forests – An Architectural Analysis*. Springer, Berlin, Germany.
- Hawthorne, W.D. (1993) *Forest Regeneration After Logging in Bia South GPR, Ghana*. ODA Forestry Series 3, Natural Resources Institute, Chatham, UK.
- Hawthorne, W.D. (1995) *Ecological Profiles of Ghanaian Forest Trees*. Tropical Forestry Paper, 29. Oxford Forestry Institute, Oxford, UK.
- Hawthorne, W.D. (1996) Holes and the sums of parts in Ghanaian Forest: regeneration, scale and sustainable use. *Proceedings of the Royal Society, Edinburgh*, **104b**, 75–176.
- Hawthorne, W.D. & Abu-Juam, M. (1995) *Forest Protection in Ghana*. IUCN, Gland, Switzerland.
- Hawthorne, W.D., Agyeman, V.K., Abu Juam, M. & Foli, E.G. (2001) *Taking stock: an annotated bibliography of logging damage and recovery in tropical forests, and the results of new research in Ghana*. Unpublished Except Via WWW, Oxford Forestry Institute, Oxford, UK.
- Hirose, T. & Werger, M.J.A. (1987) Maximizing daily carbon photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia*, **72**, 520–526.
- Horn, H.S. (1971) *The Adaptive Geometry of Trees*. Princeton University Press, New Jersey, USA.
- Hosmer, D.W. & Lemeshow, S. (1989) *Applied Logistic Regression*. Wiley, Chichester, UK.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Monographs in Population Biology 32. Princeton University Press, Princeton, USA.

- Iwasa, Y. (2000) Dynamic optimization of plant growth. *Evolutionary Ecology Research*, **2**, 437–455.
- Iwasa, Y., Cohen, D. & Leon, J.A. (1984) Tree height and crown shape, as results of competitive games. *Journal of Theoretical Biology*, **112**, 279–297.
- Jennings, S.B., Brown, N.D. & Sheil, D. (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry*, **72**, 59–73.
- Kendall, M. & Gibbons, J.D. (1990) *Rank Correlation Methods*, 5th edn. Edward Arnold, London, UK.
- King, D.A. (1996) Allometry and life history of tropical trees. *Journal of Tropical Ecology*, **12**, 25–44.
- Kohyama, T. (1993) Size-structured tree populations in gap dynamic forest – the forest architecture hypothesis for the stable coexistence of species. *Journal of Tropical Ecology*, **81**, 131–143.
- 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.
- Kyereh, B., Swaine, M.D. & Thompson, J. (1999) Effect of light on the germination of forest trees in Ghana. *Journal of Ecology*, **87**, 772–783.
- Latham, R.E. (1992) Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology*, **73**, 2129–2144.
- Lieberman, M., Lieberman, D., Peralta, R. & Hartshorn, G.S. (1995) Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *Journal of Tropical Ecology*, **11**, 161–178.
- Loehle, C. (2000) Strategy space and the disturbance spectrum: a life history model for tree species coexistence. *American Naturalist*, **156**, 14–33.
- Louviere, J.P., Meyer, R.J., Bunch, D.S., Carson, R., Dellaert, B., Hanemann, W.M., Hensher, D. & Irwin, J. (1999) Combing sources of preference data for modelling complex decision processes. *Marketing Letters*, **10**, 205–207.
- Makela, A. (1985) Differential games in evolutionary theory: height growth strategies of trees. *Theoretical Population Biology*, **27**, 239–267.
- Mardia, K.V., Kent, J.T. & Bibby, J.M. (1979) *Multivariate Analysis*. Academic Press, Duluth, London, UK.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, London, UK.
- McLachlan, G. & Krishnan, T. (1997) *EM Algorithm and Extensions*. Wiley, New York, USA.
- Montgomery, R.A. & Chazdon, R.L. (2002) Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, **131**, 165–174.
- van Nieuwstadt, M.G.L. & Sheil, D. (2005) Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *Journal of Ecology*, **93**, 191–201.
- Ostertag, R., Silver, W.L. & Lugo, A.E. (2005) Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica*, **37**, 16–24.
- Parker, G.G. (1995) Structure and microclimate of forest canopies. *Forest Canopies* (eds M.D. Lowman & N.M. Nadkri), pp. 73–106. Academic Press Inc., San Diego, California, USA.
- Poorter, L., Bongers, F., Sterck, F.J. & Wöll, H. (2003) Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology*, **84**, 60–608.
- Poorter, L., Bongers, F., Sterck, F.J. & Wöll, H. (2005) Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. *Journal of Ecology*, **93**, 256–267.
- Sack, L. & Grubb, P.J. (2001) Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Functional Ecology*, **15**, 145–154.
- Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, **113**, 447–455.
- Sheil, D. (2003) Observations of long-term change in an African rain forest. *Long-Term Changes in Tropical Tree Diversity as a Result of Natural and Man Made Disturbances: Studies from the Guiana Shield, Africa, Borneo and Melanesia* (ed. H. ter Steege), pp. 37–59. Series 22. Tropenbos, Wageningen, the Netherlands.
- Sheil, D. & Burslem, D.F.R.P. (2003) Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution*, **18**, 18–26.
- Smith, T.M. & Huston, M.A. (1989) A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, **83**, 49–69.
- Sterck, F.J., Bongers, F. & Newbery, D.M. (2001) Tree architecture in a Borneo lowland rain forest: intraspecific and interspecific differences. *Plant Ecology*, **153**, 279–292.
- Sterck, F.J., Clark, D.B., Clark, D.A. & Bongers, F. (1999) Light fluctuations, crown traits, and response delays for tree saplings in a Costa Rican lowland rain forest. *Journal of Tropical Ecology*, **1999** (15), 83–95.
- Swaine, M.D., Agyeman, V.K., Kyereh, B., Orgle, T.K., Thompson, J.T. & Veenendaal, E.M. (1997) *Ecology of Forest Trees in Ghana*. ODA Forestry Series no. 7. University of Aberdeen, Aberdeen, UK.
- Swaine, M.D. & Whitmore, T.C. (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio*, **75**, 81–86.
- Thomas, S.C. (1996a) 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. (1996b) Reproductive allometry in Malaysian rain forest trees: biomechanics versus optimal allocation. *Evolutionary Ecology*, **10**, 517–530.
- 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 Tropical Biology Series. Cambridge University Press, Cambridge, UK.
- Webb, C. & Donoghue, M. (2003) *PhyloMatic: A Database for Applied Phylogenetics (Revision R20030804)*. <http://www.phylodiversity.net/phyloMatic/>.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall International Editions, Upper Saddle River, NJ, USA.

Received 31 May 2005

revision accepted 24 November 2005

Handling Editor: David Burslem

## Supplementary material

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

**Appendix S1** Species list, number of observations and summary data.

**Appendix S2** Model fit as measured by Cox–Snell  $R^2$  (Cox & Snell 1989) and final best fit per species model parameters (i.e. for Model 2:  $f_{ij} = a_{ij} + b_{ij} \ln(\text{d.b.h.}) + c_{ij} \text{d.b.h.}$ , where  $j$  is the species label, see Methods) for small (5–20 cm d.b.h.) and large (30–80 cm d.b.h.) stems.