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Douglas Sheil

Center for International Forestry Research, Indonesia

Agus Salim

Center for International Forestry Research, Jakarta

Jérôme Chave

Laboratoire Evolution et Diversité Biologique, Toulouse, France

Jerome K. Vanclay

Southern Cross University

William D. Hawthorne

University of Oxford

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Illumination-size relationships of 109 coexisting tropical forest trees

Douglas Sheil¹, Agus Salim¹, Jérôme Chave², Jerome Vanclay³, William D. Hawthorne⁴

1. Center for International Forestry Research, P.O. Box 6596 JKPWB, Jakarta 10065, Indonesia.

2. Laboratoire Evolution et Diversité Biologique, UMR CNRS 5174, 118, route de Narbonne, F-31062 Toulouse, France.

3. School of Environmental Science and Management, Southern Cross University, PO Box 157, Lismore NSW 2480, Australia.

4. Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK.

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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 inter-specific 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 5cm dbh, 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 dbh drop to the lowest illumination quartile at 40cm dbh, 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. Apparently quite similar species can therefore remain ecologically distinct over their lifetimes.

Introduction

Many studies have highlighted the importance of inter-specific differences in light requirement for understanding species coexistence in tropical rain forest trees (Ashton 1998, Brown *et al.* 1999, Clark and Clark 1992, Dalling *et al.* 1998, Turner 2001, Sterck *et al.* 2001), and schemes for grouping species are often based on illumination requirements alone (Swaine and Whitmore 1988, Hawthorne 1995). Ecological theory has also emphasized the role of variation in the light requirements of co-existing 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 inter-specific 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 and Clark 1992, Grubb 1977, Parker 1995, Hawthorne 1995, Montgomery & Chazdon 2002).

Ability to grow and shade-out competitors varies with conditions. Partitioning of the light environment among species can promote co-existence (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 (Sterk *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 that to best persist in low light, plants must maximise photon capture and minimise carbon expended. Low photosynthetic capacity is beneficial because it is less costly, but this leaves the plant poorly equipped to utilise 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: though 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 and 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 data-set and a range of analyses. We consider how crown exposure varies in relation to stem diameter, and how this varies amongst species: are there discernable 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 were established since the 1920s and have been subjected to various interventions (see Hawthorne & Abu-Juam 1995). Annual rainfall ranges from 1000 mm to 2250mm. 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 ≥ 30 cm diameter were measured. Stems ≥ 5 cm and ≥ 10 cm diameter were recorded in 0.05 ha and 0.1 ha sub-plots, respectively (Hawthorne, 1995). Stem diameters (dbh) were recorded, at 1.3m height or above any buttresses or deformations. Buttressing

and fluting were not a serious concern for stems below 40 cm dbh. 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 1. 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°), 3 = fully exposed from above (other than as 4), 2 = partly exposed to direct light or 1 = fully overshadowed (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 (a) the broad area sampled (avoiding biases from specific histories) (b) the fact that areas with low tree cover provide few trees to the analysis, and (c) 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) 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 ($i = 1..4$) 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 $p_4 = 1 - p_1 - p_2 - p_3$ (n.b. results are independent of the exposure class designated as analytically redundant). The function f_i defines the relationship between dbh 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 (dbh 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 -value ≤ 0.05 (Burnham and Anderson, 1998). We fitted models of exposure class with linear, logarithmic, quadratic and cubic terms for dbh. 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 discernable species-specific effects within the crown exposure-diameter relationships. To explore this we fitted two models:

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

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

Where $\ln(d)$ is the natural logarithm of stem diameter d , 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 dbh 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 2.

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 (p95) diameter for all stems ≥ 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 dbh) and observations of larger trees (>20cm DBH), 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 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 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 and 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) x (probability that the species has mean score of m , given it belongs to group A) (i.e. $P(A|m) = P(A).P(m|A)/\text{constant}$). 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 the species within this range are classed as members.

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

To test for minimum, maximum and other specific size exposure patterns we used bootstrapped model estimates. The bootstrap sample is constructed as follows: at each observed dbh (per cm), we sample (with replacement) the crown exposure score. The sample size at each dbh is the number of observed stems at that dbh. This process is repeated for every observed dbh. The collated sample is then used to estimate the model and, using the model parameter estimates, E is computed across dbh and the existence/non-existence of local minima/maxima is recorded. P-values were estimated as the proportion of 1000 bootstrapped models that do not exhibit such behaviour (Efron and Tibshirani, 1994).

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 branchpoint 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; see appendix 3).

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-value < < 0.001). M2 is also better than M1 for the 30-80 cm interval (243934.5 vs. 284369.3, p-value < < 0.001). This result confirms significant variation amongst species and justifies modelling them individually (see appendix 2 for full model details). Examples of observed and modelled mean crown exposures for two species are shown in Figure 1. In fact, up to 60 cm dbh, the fit is remarkably good for all species despite the noise and over-dispersion evident in the data.

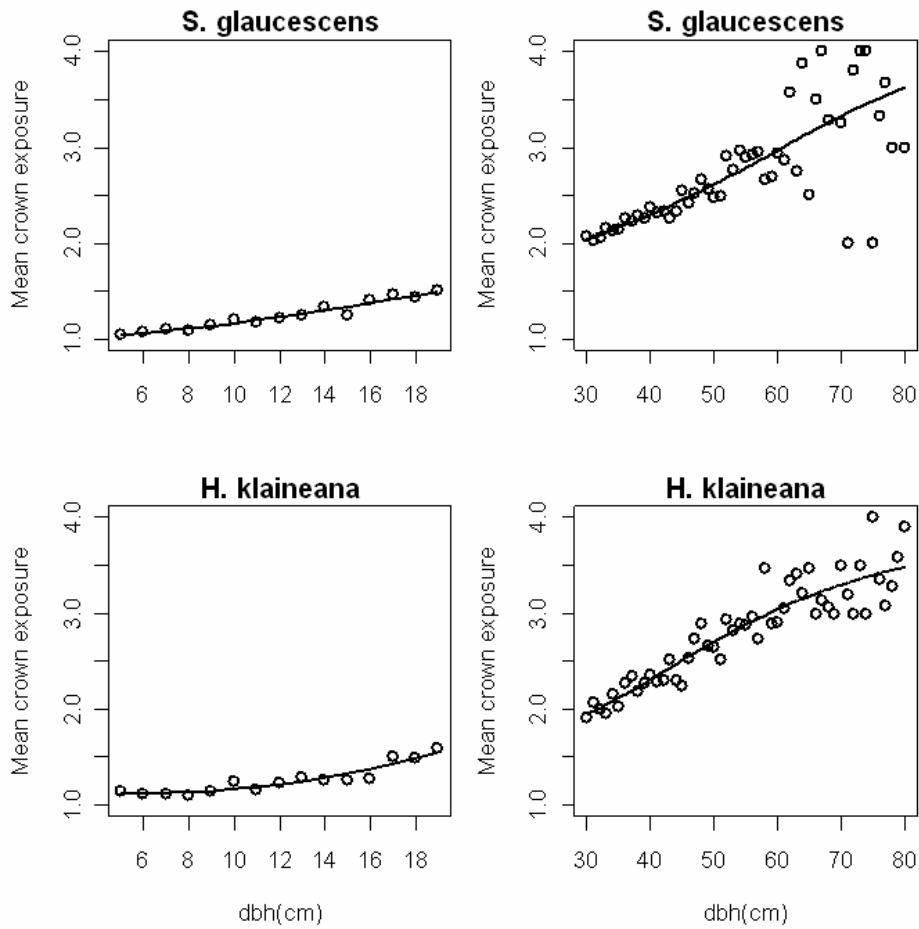


Figure 1. Observed (circles, mean value of observation in cm-interval) and modelled (line) mean crown exposures for two example species: *Strombosia glaucescens*, a species with few large diameter observations, (Cox-Snell $R^2 = 0.882$) and *Hannoa klaineana*, a well represented species (Cox-Snell $R^2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

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 dbh, and reveal a monotonic increase in likelihood of being recorded in better-illumination as their diameter increases. We observed local minima for 6 species. Bootstrapped model estimates (*see methods*) found these were significant only in *Nauclea diderrichii* (minimum exposure occurs at approx. 11 cm dbh, p-value = 0.044), and *Holoptelea grandis* (approx. at 9 cm dbh, p-value = 0.008). We know that these species regenerate in large-gaps or tend to be more abundant in secondary forests (Hawthorne 1996). Figure 2a 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 dbh (Figure 2c).

Panda oleosa is the only species with a local maximum at lower dbh (Figure 2c, at approximately dbh = 15 cm, but note that exposure climbs with increasing diameter > 30 cm dbh, Figure 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 dbh = 77 cm (below *max-d* for this species, which is 97 cm) but the bootstrap p-value is not significant (p-value = 0.356). *Carapa procera* yields a similarly non-significant pattern (p-value = 0.501). Model-fits for all 109 species are shown in Figure 3.

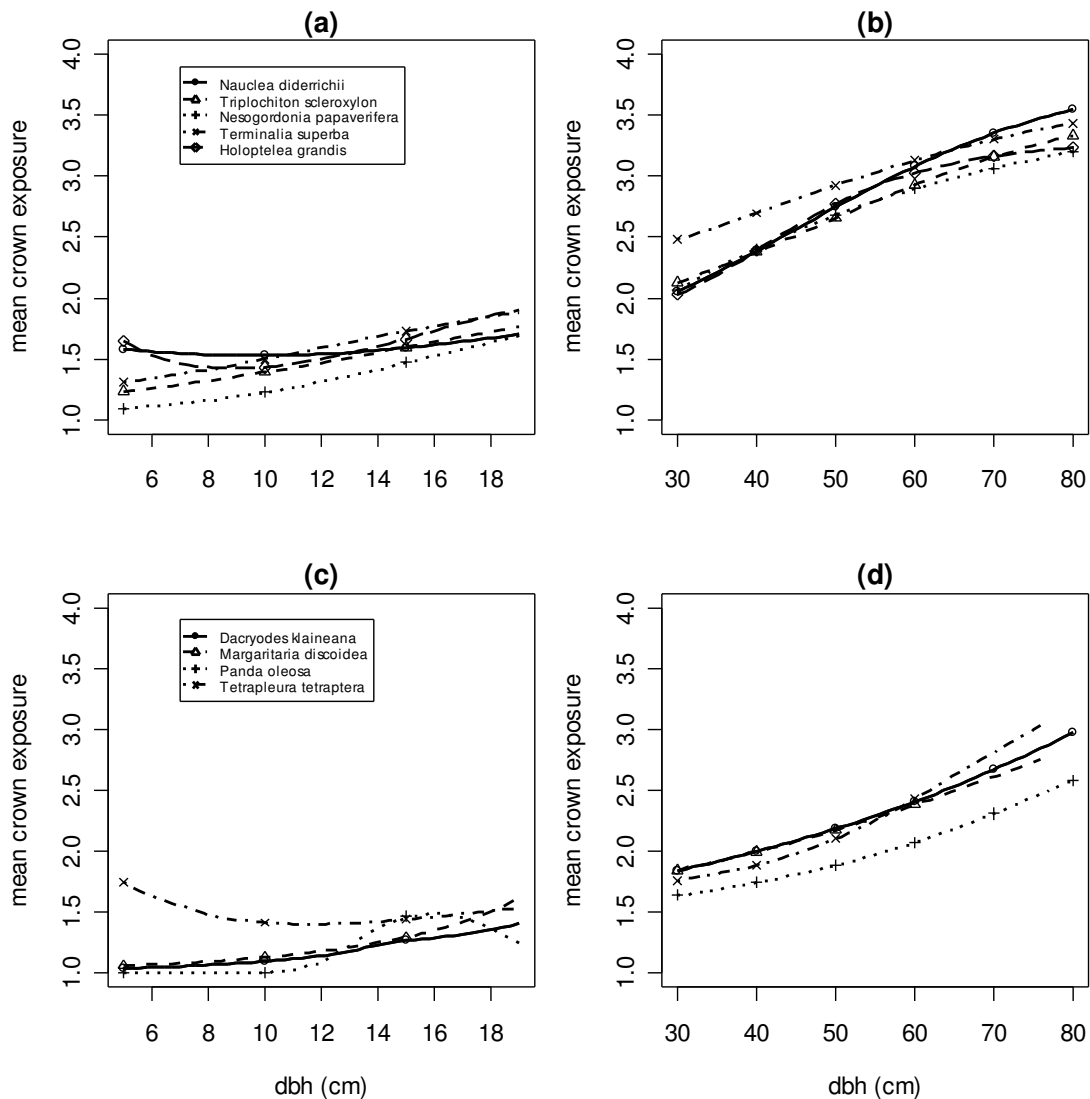


Figure 2. Modelled exposure-diameter relationship for nine species. Left panels show the relationship at small diameter (5-20 cm), while right panels show it at large diameter (30-80 cm).

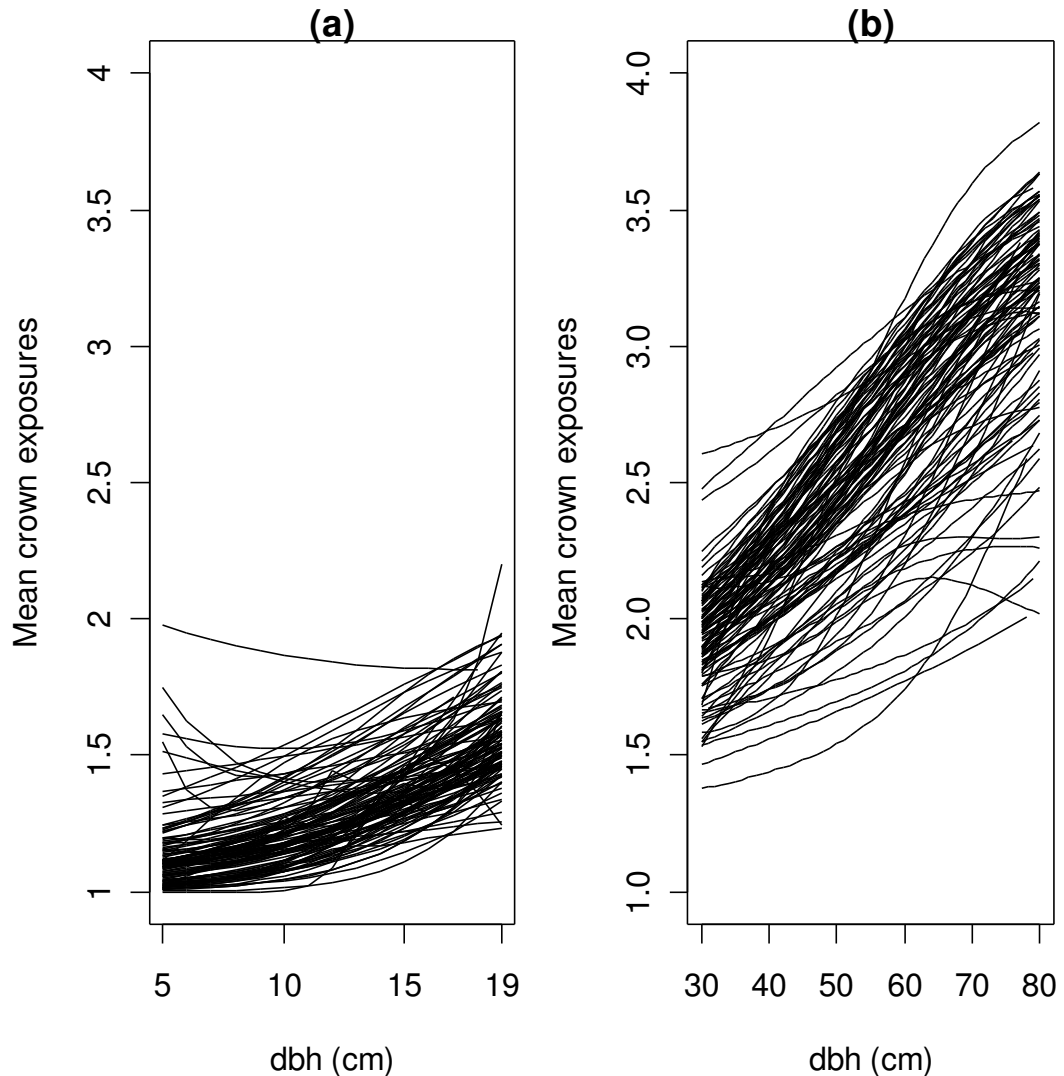


Figure 3. The modelled mean crown exposures profiles for all 109 species.

Natural species groups

The mean E_{10} and E_{40} values i.e. estimated mean exposures at dbh 10cm and 40cm 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 dbh as others are at 40 cm.

The 'model-mean crown-exposure' (E_d) distribution for the 109 species appears both peaked and broadly distributed. At 10 cm dbh (Fig 4), this distribution

is better described as a mixture of two normal distributions than one (likelihood ratio test, p -value < 0.005) implying a significantly bimodal distribution. Adding further Normal distributions decreases fit. Accepting this bimodal model as a basis for dividing species species are 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*₁₀, accounts for 88 of the 109 species and comprises all Hawthorne's shade-bearers and most NPLDs (39 species), but also some pioneers (10) and swamp species (4 species) (mean = score 1.17, se = 0.07). The less shaded group, which we call *more-exposed*₁₀ (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*₁₀ 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} (Kruskall-Wallis test p -value = 0.002, members of the *more-exposed*₁₀ remain more exposed also at 40 cm) and by their net difference in E between 10 and 40 dbh (p -value = 0.025, *less-exposed*₁₀ members shows greater change). Though the mean *max-d* values for the *more-exposed*₁₀ group are slightly higher than the *less-exposed*₁₀ (88 versus 84 cm) this patterns was not significant (Kruskall-Wallis test, p -value = 0.695).

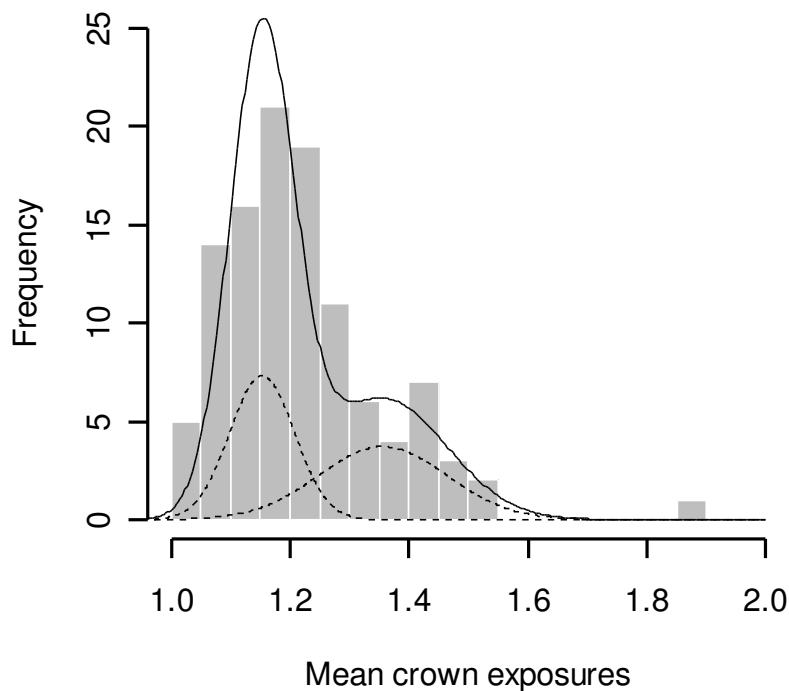


Figure 4. Histogram of modelled mean crown exposures. The solid curve is predicted number of species in each bin, calculated using a mixture of two Normal densities (Likelihood ratio test of simple Normal density vs. mixture, $\chi^2 = 14.12$, p-value < 0.005). The dashed curves are un-scaled densities 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 $E_{10} = 1.32$.

Cross-species ranking of mean exposure

Taking all 109 species, inter-specific exposure rankings remained significant across stem-sizes (Kendall's tau correlation coefficient, τ , for 10 versus 40 cm diameter, 0.338, p-value < 0.001). If the analysis is confined to the *less-exposed*₁₀ species the correlation remains significant ($\tau = 0.294$, p-value < 0.001, n = 88). If the analysis is confined to the *more-exposed*₁₀ species the correlation is positive but only marginally significant ($\tau = 0.276$, p-value = 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-value < 0.0001, on 61 species with > 50 individuals in both 10-15 cm and 40-45 cm classes, *see Analysis*). The significant result persisted when data

from all potentially problematic plots (disturbed, swampy, rocky) were excluded (136,743 identified trees, comprising 31 species were included, p -value < 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 -value < 0.005; wet: 27 species, p -value < 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 dbh—this division is intended only as a descriptive and heuristic approach (N.B. 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 dbh in the same quartile (25% exposure group) as their 10 cm dbh values (i.e. they tend to maintain their relative exposure status; Figure 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 (Figure 5, top right). Bootstrapping suggests that this trend is significant for *R. brevicuspe* (p -value = 0.019) (i.e. 98.1% of bootstrapped curves show this pattern) but not for *I. gabonensis* or *K. gabonensis* (p -value = 0.348 and p -value = 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 (Figure 5, bottom left; bootstrap estimates p -value = 0.088 and p -value = 0.106 respectively).

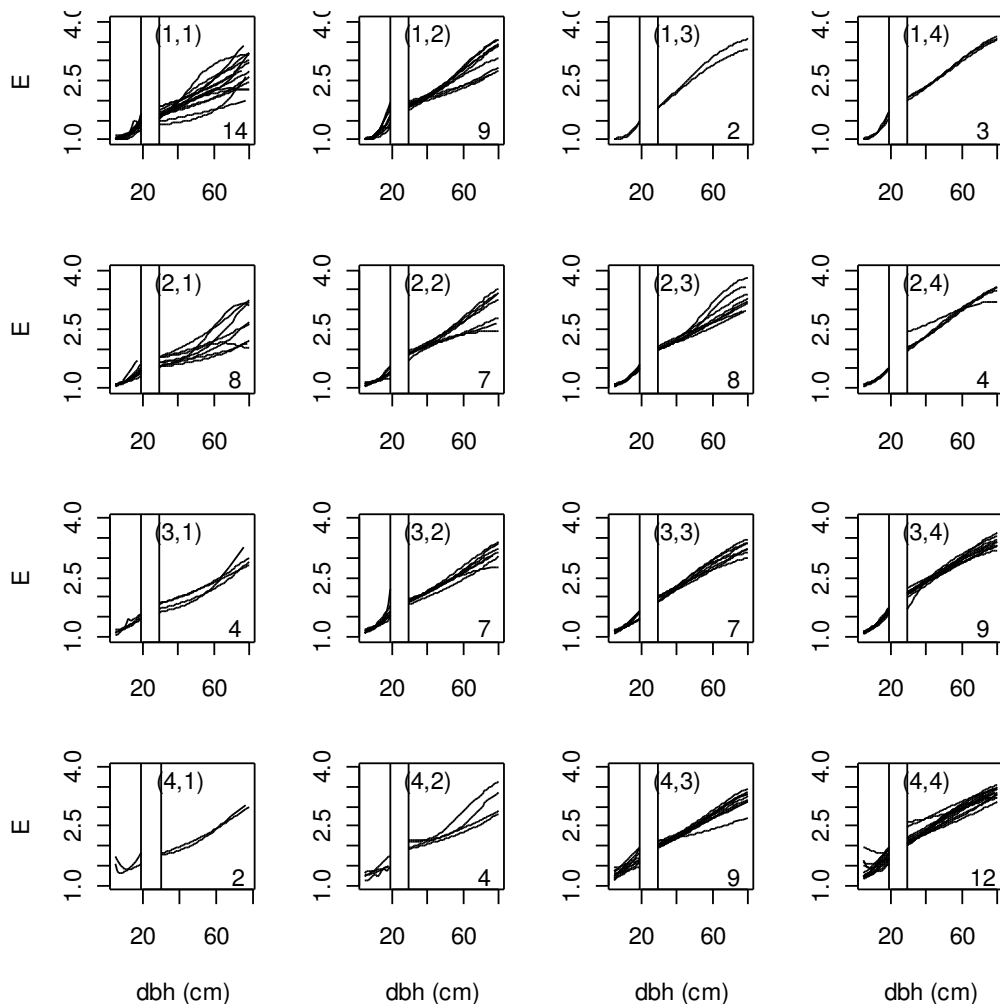


Figure 5. Modelled mean crown exposure, E , versus stem diameter for species groupings based on transitions between quartiles of modelled mean crown exposures at 10 and 40 cm dbh (E_{10} and E_{40}). The horizontal axis is dbh (cm) and the vertical axis is E , modelled mean crown exposure. For each group, the coordinate at the centre top is the quartile at 10 and 40 cm dbh 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 dbh. 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 3 graphs in the lower left corner (10 species) switch from high to low E , the three graphs in the upper right corner (9 species) switch from low to high E .

The 16 transition categories (Figure 5) had clear relationships with Hawthorne's 3 principle guild categories (see Fig 6). Pioneers predominate in the upper exposure quartile at both 10 and 40 cm dbh (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.

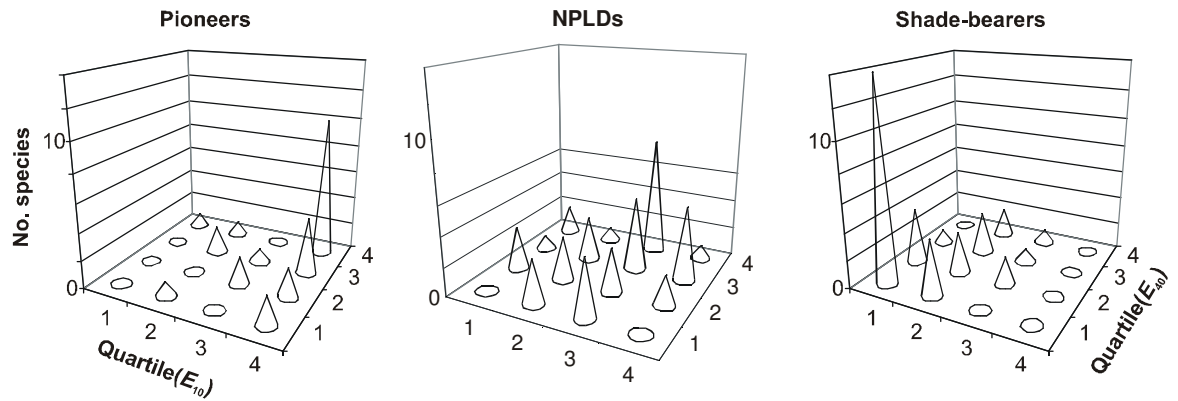


Figure 6. The distribution of the species by the main Hawthorne guild and by the quartiles in which their exposures are modelled at 10 and 40 cm dbh (E_{10} and E_{40}).

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 (Figure 7, at 10 cm dbh, $\tau = 0.156$, p-value = 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*₁₀ group (at 40 cm $\tau = 0.336$, p-value < 0.001, at 10 cm, $\tau = 0.212$ p-value = 0.004 n = 88). For the *more-exposed*₁₀ group, the correlations though positive were significant only at large size ($\tau = 0.024$, p-value = 0.880 at 10 cm and $\tau = 0.320$, p-value = 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 dbh) were also those that reached the largest sizes ($\tau = 0.291$, p-value < 0.001, n = 109).

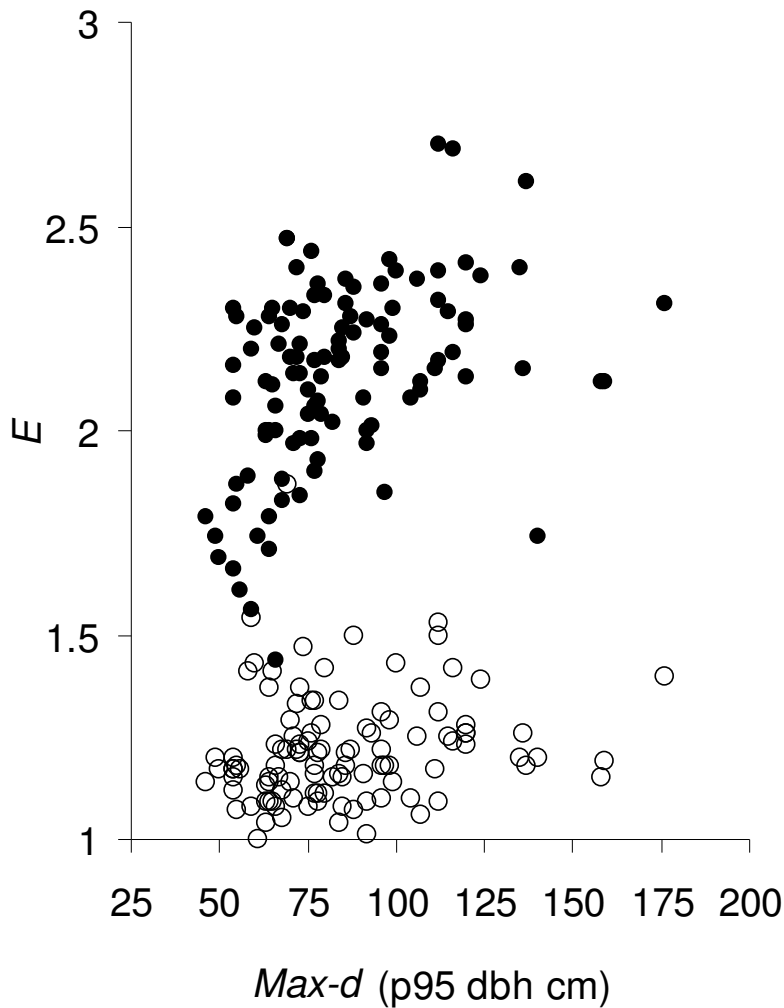


Figure 7. Modelled exposure, E , at 10 cm (E_{10} open circles) and 40 cm dbh (E_{40} closed circles) for 109 species versus $Max-d$ (p95 dbh of the per-species sample tree population with stems over 30 cm dbh).

Phylogeny

Regression that partitions variation by phylogenetically independent contrasts (see methods), using 166 branch points (Appendix 3) shows that the $max-d$ versus E relationship is positive and significant across the phylogeny (i.e. at dbh 10-cm: p-value = 0.026, and at 40-cm p-value = 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-value = 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 -value = 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 ≥ 30 dbh regardless of species from plots with ≥ 25 such trees; the mean per-plot p95 values for wet, moist and dry are 51.29 ± 0.31 , 52.54 ± 0.23 , and 54.06 ± 0.28 , with $n = 193, 741$, and 380 plots, all contrasts significant, p -value < 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 sub-canopy sized trees of any species occur in a wide range of illumination conditions. The strength of our modelling lies in the ability to summarise 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_d , 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 Figure 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.* (2003)'s 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-value = 0.012, $n = 11$) and our E_{40} (p-value = 0.006). E_{40} is also significantly rank correlated with the Liberian measure of light demand (% trees in high light between 10 & 20 cm dbh, p-value = 0.005), tree height₁₅ (tree specific regressions for a tree of dbh 15 cm, p-value = 0.036) and marginally related to the inverse of crown depth₁₅ (p-value = 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 and 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 dbh). However, in our study mean E_{10} values span 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 dbh (1.2 to 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 inter-specific 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 (Figure 4) is consistent with two overlapping groups of species with 88 species in the *less-exposed*₁₀ groups and 21 in the more broadly distributed *more-exposed*₁₀ 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 versus 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*₁₀ grouping. *N. 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*, *Terminalia superba*) are in our *more-exposed*₁₀ group and five (*Guarea cedrata*, *Khaya ivorensis*, *Lovoa trichilioides*, *Pterygota macrocarpa*, *Sterculia rhinopetala*) are in our *less-exposed*₁₀ 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*₁₀ group (all but *Terminalia ivorensis*) but in only one

(*Khaya ivorensis*) of the *less-exposed*₁₀ group. This pattern is close to significant (Fishers exact test, p-value = 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 and 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 dbh (Figure 2c). We cannot identify an artefact in this result: *P. oleosa* is well recorded with 1347 observations, is distinctive and readily identified. This elephant-dispersed species has a very clear architecture with 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 dbh and in the highest at 40 cm dbh. 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 (c.f. Sheil 2003 for Uganda),

and there is evidence in other parts of the world that shorter colonizing species preempt 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 Figure 3—our detection of structure in the variation shows that co-existing tree species are not equivalent through ontogeny. Of course, with many co-existing 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 their large size because of 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 (Hirose and Werger 1987, Field and Mooney 1986, 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 (Westoby *et al.* 2002, Givnish 1988, 1995). 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 versus 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 may 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 rainforests struck by extreme droughts, large-stems may suffer higher relative mortality than small stems (e.g. van Nieuwstadt & Sheil 2005) similarly wind storms generally take a greater toll of large 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). 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, Kohyama *et al.* 2003). We predict that the apparency of a species-maximum-size versus 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 distinct, and 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 realisation 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.

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References

- 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 Trans. Aut. Cont.*, **19**, 716-723.
- 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.

- 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., 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.
- 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.
- 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 Ed. Chapman and 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* in 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. *Aust. J. 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 and Hall, New York, USA.
- Grafen, A. (1989) The phylogenetic regression. *Phil. Trans. R. Soc. Lond* 205:581-98 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, R.A.A. Oldeman, & P.B. Tomlinson (1978) *Tropical Trees and Forests - An architectural analysis*. Springer, Berlin, Germany
- Hawthorne, W.D. (1993) *Forest regeneration after logging in Bia South GPR, Ghana*. O.D.A. 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.
- 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 ed. 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) Combining 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 edition. Chapman and 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.
- Ostertag, R., Silver, .WL. & 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, in: *Forest Canopies* (eds. Lowman, M. D. & Nadkri, N. M.) 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 Hans ter Steege), pp. 37-59. Tropenbos Series 22, 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., 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.
- 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.
- Swaine, M.D. & Whitmore, T.C. (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio*, **75**, 81-86.
- 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
- 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.
- 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
- Webb, C. & Donoghue, M. (2003) Phylomatic: a database for applied phylogenetics (revision R20030804), available on-line at <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 & Systematics*, **33**, 125-159.
- Zar, J. H. (1996) *Biostatistical Analysis*. Third edition. Prentice Hall International Editions, Upper Saddle River, NJ, USA.

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Appendix 1. Species list, number of observations and summary data.

¹ Species	Family	² N	³ Max-d (cm)	⁴ N ₈₀	⁵ E ₁₀	⁶ E ₄₀	⁷ H Guild	⁸ E ₁₀ class	⁹ Transition class
<i>Afrosersalisia</i> (= now <i>Synsepalum</i>) <i>afzelii</i>	Sapotaceae	511	92	35	1.01	1.97	S	C	1:1
<i>Albizia adianthifolia</i>	Mimosaceae	507	80	21	1.42	2.18	N	H	4:3
<i>Albizia zygia</i>	Mimosaceae	981	88	78	1.50	2.24	N	H	4:3
<i>Allanblackia parviflora</i>	Euphorbiaceae	2389	54	4	1.15	2.08	S	C	2:2
<i>Alstonia boonei</i>	Apocynaceae	2146	120	468	1.26	2.13	P	C	3:2
<i>Amphimas pterocarpoides</i>	Caesalpiniaceae	1381	99	122	1.14	2.30	N	C	2:4
<i>Anogeissus leiocarpa</i>	Combretaceae	266	69	5	1.87	2.47	X	H	4:4
<i>Anopyxis klaineana</i>	Rhizophoraceae	289	112	79	1.31	2.17	N	C	4:2
<i>Anthonotha macrophylla</i>	Caesalpiniaceae	701	78	12	1.09	1.93	S	C	1:1
<i>Anthostema aubryanum</i>	Euphorbiaceae	411	65	1	1.09	2.11	W	C	1:2
<i>Antiaris toxicaria</i>	Moraceae	2941	120	660	1.26	2.41	N	C	3:4
<i>Antrocaryon micraster</i>	Anacardiaceae	453	98	55	1.18	2.23	N	C	2:3
<i>Beilschmiedia mannii</i>	Lauraceae	1430	64	5	1.14	2.00	S	C	2:1
<i>Berlinia confusa</i>	Caesalpiniaceae	722	84	42	1.04	2.20	S	C	1:3
<i>Bombax buonopozense</i>	Bombacaceae	518	96	57	1.31	2.36	P	C	4:4
<i>Buchholzia coriacea</i>	Capparaceae	366	54	2	1.12	1.82	S	C	1:1
<i>Bussea occidentalis</i>	Caesalpiniaceae	1406	73	33	1.23	1.98	N	C	3:1
<i>Calpocalyx brevibracteatus</i>	Mimosaceae	2931	54	5	1.20	2.16	S	C	3:2
<i>Canarium schweinfurthii</i>	Burseraceae	326	115	51	1.25	2.29	N	C	3:4
<i>Carapa procera</i>	Meliaceae	5488	46	3	1.14	1.79	S	C	1:1
<i>Ceiba pentandra</i>	Bombacaceae	2886	176	1207	1.40	2.31	P	H	4:4
<i>Celtis adolfi-friderici</i>	Ulmaceae	2909	84	140	1.16	2.17	P	C	2:3
<i>Chidlowia sanguinea</i>	Caesalpiniaceae	690	66	8	1.08	1.44	S	C	1:1
<i>Chrysophyllum perpulchrum</i>	Sapotaceae	1636	82	89	1.15	2.02	N	C	2:2

¹ Species	Family	² N	³ Max-d (cm)	⁴ N ₆₀	⁵ E ₁₀	⁶ E ₄₀	⁷ H Guild	⁸ E ₁₀ class	⁹ Transition class
<i>Chrysophyllum pruniforme</i>	Sapotaceae	210	104	35	1.10	2.08	S	C	1:2
<i>Cleistopholis patens</i>	Annonaceae	1243	70	21	1.29	2.30	P	C	4:4
<i>Coelocaryon oxycarpum</i>	Myristicaceae	278	71	4	1.25	2.14	N	C	3:2
<i>Copaifera salikounda</i>	Caesalpiniaceae	289	137	22	1.18	2.61	S	C	2:4
<i>Corynanthe pachyceras</i>	Rubiaceae	4818	56	5	1.17	1.61	N	C	2:1
<i>Coula edulis</i>	Olacaceae	672	68	9	1.05	1.88	S	C	1:1
<i>Cylicodiscus gabunensis</i>	Mimosaceae	933	159	467	1.19	2.12	S	C	2:2
<i>Cynometra ananta</i>	Caesalpiniaceae	1844	87	145	1.22	2.28	S	C	3:3
<i>Dacryodes klaineana</i>	Burseraceae	7006	63	41	1.09	2.00	S	C	1:1
<i>Dialium aubrevillei</i>	Caesalpiniaceae	3498	78	99	1.11	2.07	S	C	1:2
<i>Dichapetalum guineense</i> (now <i>D. madagascariense</i>)	Dichapetalaceae	600	59	1	1.08	1.56	S	C	1:1
<i>Discoglyprena caloneura</i>	Euphorbiaceae	1641	64	4	1.37	2.28	P	H	4:3
<i>Distemonanthus benthamianus</i>	Caesalpiniaceae	856	98	71	1.29	2.42	N	C	4:4
<i>Duboscia viridiflora</i>	Tiliaceae	336	135	148	1.20	2.40	N	C	3:4
<i>Entandrophragma angolense</i>	Meliaceae	2644	96	245	1.18	2.26	N	C	2:3
<i>Entandrophragma cylindricum</i>	Meliaceae	1116	120	257	1.28	2.26	N	C	4:3
<i>Entandrophragma utile</i>	Meliaceae	467	136	100	1.26	2.15	N	C	3:2
<i>Erythroxylum mannii</i>	Erythroxylaceae	230	79	9	1.22	2.13	P	C	3:2
<i>Gilbertiodendron limba</i>	Caesalpiniaceae	1044	75	21	1.08	2.04	W	C	1:2
<i>Guarea cedrata</i>	Meliaceae	1921	85	76	1.15	2.18	S	C	2:3
<i>Guarea thompsonii</i>	Meliaceae	433	75	6	1.24	2.10	S	C	3:2
<i>Guibourtia ehie</i>	Caesalpiniaceae	870	78	27	1.21	2.36	N	C	3:4
<i>Hannoa klaineana</i>	Simaroubaceae	3474	86	123	1.18	2.31	P	C	2:4
<i>Heritiera utilis</i>	Sterculiaceae	1589	85	103	1.08	2.25	N	C	1:3
<i>Hexalobus crispiflorus</i>	Annonaceae	1192	91	71	1.16	2.08	S	C	2:2
<i>Holarrhena floribunda</i>	Apocynaceae	324	65	2	1.41	2.30	P	H	4:4

¹ Species	Family	² N	³ Max-d (cm)	⁴ N ₆₀	⁵ E ₁₀	⁶ E ₄₀	⁷ H Guild	⁸ E ₁₀ class	⁹ Transition class
<i>Holoptelea grandis</i>	Ulmaceae	518	100	91	1.43	2.39	P	H	4:4
<i>Homalium letestui</i>	Flacourtiaceae	800	69	5	1.22	2.47	N	C	3:4
<i>Irvingia gabonensis</i> (now <i>I. wombolu</i>)	Irvingiaceae	971	80	31	1.11	2.33	N	C	1:4
<i>Khaya ivorensis</i>	Meliaceae	1369	120	322	1.23	2.27	N	C	3:3
<i>Klainedoxa gabonensis</i>	Irvingiaceae	998	112	173	1.09	2.32	N	C	1:4
<i>Lannea welwitschii</i>	Anacardiaceae	1304	77	45	1.34	2.33	P	H	4:4
<i>Leptaulus daphnoides</i>	Icacinaceae	526	68	1	1.12	1.83	S	C	1:1
<i>Lonchocarpus sericeus</i>	Papilionaceae	302	77	10	1.11	2.06	N	C	1:2
<i>Lophira alata</i>	Ochnaceae	336	97	47	1.18	1.85	P	C	2:1
<i>Lovoa trichilioides</i>	Meliaceae	453	106	74	1.25	2.37	N	C	3:4
<i>Mammea africana</i>	Guttiferae	677	96	58	1.10	2.15	S	C	1:2
<i>Mansonia altissima</i>	Sterculiaceae	1609	74	37	1.47	2.29	N	H	4:3
<i>Margaritaria discoidea</i>	Euphorbiaceae	322	76	8	1.34	1.98	P	H	4:1
<i>Millettia rhodantha</i>	Papilionaceae	571	63	2	1.13	1.99	S	C	1:1
<i>Monodora myristica</i>	Annonaceae	1264	64	10	1.15	1.71	S	C	2:1
<i>Morus mesozygia</i>	Moraceae	704	77	16	1.18	2.17	P	C	2:3
<i>Musanga cecropioides</i>	Moraceae	2424	59	3	1.54	2.20	P	H	4:3
<i>Myrianthus arboreus</i>	Annonaceae	1721	50	2	1.17	1.69	S	C	2:1
<i>Nauclea diderrichii</i>	Rubiaceae	394	112	114	1.53	2.39	P	H	4:4
<i>Nesogordonia papaverifera</i>	Sterculiaceae	7110	72	149	1.22	2.40	S	C	3:4
<i>Ongokea gore</i>	Olacaceae	417	84	21	1.34	2.22	N	H	4:3
<i>Pachypodanthium staudtii</i>	Annonaceae	678	70	2	1.14	2.18	N	C	2:3
<i>Panda oleosa</i>	Pandaceae	1347	61	3	1.00	1.74	S	C	1:1
<i>Parinari excelsa</i>	Chrysobalanaceae	1067	107	123	1.06	2.12	N	C	1:2
<i>Parkia bicolor</i>	Mimosaceae	1831	111	350	1.17	2.15	N	C	2:2
<i>Pentaclethra macrophylla</i>	Mimosaceae	1017	92	81	1.09	2.00	N	C	1:2

¹ Species	Family	² N	³ Max-d (cm)	⁴ N ₆₀	⁵ E ₁₀	⁶ E ₄₀	⁷ H Guild	⁸ E ₁₀ class	⁹ Transition class
<i>Pentadesma butyracea</i>	Guttiferae	1416	63	8	1.04	2.12	S	C	1:2
<i>Petersianthus macrocarpus</i>	Lecythidaceae	3676	96	453	1.22	2.19	P	C	3:3
<i>Rhodognaphalon brevicuspe</i>	Bombacaceae	910	88	74	1.07	2.35	P	C	1:4
<i>Phyllocosmus sessiliflorus</i>	Ixonanthaceae	824	73	13	1.21	1.84	N	C	3:1
<i>Piptadeniastrum africanum</i>	Mimosaceae	5743	116	1244	1.24	2.19	N	C	3:3
<i>Protomegabaria stapfiana</i>	Euphorbiaceae	2277	64	15	1.09	1.79	S	C	1:1
<i>Pterygota macrocarpa</i>	Sterculiaceae	2840	92	323	1.27	2.27	N	C	3:3
<i>Pycnanthus angolensis</i>	Myristicaceae	4227	86	335	1.21	2.37	N	C	3:4
<i>Ricinodendron heudelotii</i>	Euphorbiaceae	2414	107	350	1.37	2.10	P	H	4:2
<i>Sacoglottis gabonensis</i>	Humiriaceae	213	140	98	1.20	1.74	N	C	2:1
<i>Scottellia klaineana</i>	Flacourtiaceae	3888	67	38	1.15	2.21	S	C	2:3
<i>Scytopetalum tieghemii</i>	Scytopetalaceae	2148	55	4	1.07	1.87	S	C	1:1
<i>Spondianthus preussii</i>	Euphorbiaceae	318	66	4	1.18	2.06	W	C	2:2
<i>Sterculia oblonga</i>	Sterculiaceae	2799	76	81	1.26	2.44	N	C	3:4
<i>Sterculia rhinopetala</i>	Sterculiaceae	5009	68	73	1.22	2.26	N	C	3:3
<i>Sterculia tragacantha</i>	Sterculiaceae	1618	60	2	1.43	2.25	P	H	4:3
<i>Stereospermum acuminatissimum</i>	Bignoniaceae	315	73	6	1.37	2.14	P	H	4:2
<i>Strephonema pseudocola</i>	Combretaceae	337	71	2	1.10	1.97	S	C	1:1
<i>Strombosia glaucescens</i>	Olacaceae	1129 6	54	11	1.17	2.30	S	C	2:4
<i>Terminalia ivorensis</i>	Combretaceae	481	116	132	1.42	2.69	P	H	4:4
<i>Terminalia superba</i>	Combretaceae	2618	112	809	1.50	2.70	P	H	4:4
<i>Tetrapleura tetraptera</i>	Mimosaceae	470	58	2	1.41	1.89	P	H	4:1
<i>Tieghemella heckelii</i>	Sapotaceae	451	158	90	1.15	2.12	N	C	2:2
<i>Treculia africana</i>	Moraceae	1106	79	41	1.28	2.04	N	C	4:2
<i>Trichilia martineauii</i>	Meliaceae	2715	49	1	1.20	1.74	N	C	3:1
<i>Trichilia prieureana</i>	Meliaceae	7012	54	5	1.17	1.66	N	C	2:1

¹ Species	Family	² N	³ Max-d (cm)	⁴ N ₈₀	⁵ E ₁₀	⁶ E ₄₀	⁷ H Guild	⁸ E ₁₀ class	⁹ Transition class
<i>Trichilia tessmannii</i>	Meliaceae	1141	73	19	1.21	2.21	N	C	3:3
<i>Trilepisium madagascariense</i>	Moraceae	2720	66	41	1.23	2.00	N	C	3:1
<i>Triplochiton scleroxylon</i>	Sterculiaceae	9251	124	2979	1.39	2.38	P	H	4:4
<i>Turraeanthus africanus</i>	Meliaceae	4812	77	156	1.16	1.90	S	C	2:1
<i>Xylocarpus evansii</i>	Mimosaceae	870	93	67	1.26	2.01	N	C	3:2
<i>Xylocarpus staudtii</i>	Annonaceae	1164	55	2	1.18	2.28	S	C	2:3
<i>Zanthoxylum gillettii</i>	Rutaceae	258	72	5	1.33	2.18	P	H	4:3

¹ Nomenclature follows Hawthorne (1995) which provides full authorities.

Caesalpiniaceae, Papilionaceae and Mimosaceae are now more usually considered together in the Leguminosae.

² Number of stems diameter greater than or equal to 5 cm.

³ This is the 95th percentile of stems recorded over 30 cm diameter in closed forest.

⁴ Number of stems diameter \geq 80 cm.

⁵ GLM derived mean exposure class where $d = 10$ cm.

⁶ GLM derived mean exposure class where $d = 40$ cm.

⁷ H-Guild guilds as described by Hawthorne (1995) p-value = Pioneer, S = Shade-bearer, N = Non pioneer light demander, W = Swamp, X = savanna

⁸ GLM derived mean exposure class where $d = 10$ cm (E_{10}) divided into two apparent guilds based on the best-fit model resolution of all the species E_{10} observations into two (overlapping) Normal distributions. Species are allocated to the groups with the mean to which their own modelled E_{10} values are closest. The less shaded (*more-*

*exposed*₁₀) members are labelled H (heliophile) and more shaded (*less-exposed*₁₀) are labelled C (covered).

⁹ Quartiles of modelled mean crown exposures at 10 cm dbh (first number 1-4 lower to higher) and 40 cm dbh (second number).

Appendix 2. 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: $f_{ij} = a_{ij} + b_{ij} \ln(\text{dbh}) + c_{ij} \text{dbh}$, where j is the species label, see methods) for small (5-20 cm dbh) and large (30-80 cm dbh) stems.

Name	Cox-		a_1	b_1	c_1	a_2	b_2	c_2	a_3	b_3	c_3
	Snell R^2	Stems									
<i>Afrosorsalisia afzelii</i>	0.84	Small	-2.939	5.033	-0.249	-0.344	-1.613	0.629	4.588	-0.108	-5.128
		Large	-0.247	1.340	1.596	-0.772	0.896	1.663	-0.181	0.001	1.704
<i>Albizia adianthifolia</i>	0.69	Small	1.035	2.755	-0.449	-0.891	2.005	-0.188	-0.302	-0.611	-0.157
		Large	0.424	-0.080	-0.025	0.290	0.582	-0.038	-0.049	-1.336	0.081
<i>Albizia zygia</i>	0.594	Small	-0.162	0.653	0.305	-1.560	0.625	0.390	1.353	-0.030	-0.361
		Large	-0.324	0.144	-1.890	0.008	0.303	-0.016	0.760	-1.103	0.055
<i>Allanblackia floribunda</i>	0.825	Small	4.120	-0.491	0.043	-1.859	0.986	0.105	-0.930	1.401	-1.078
		Large	0.383	-0.879	0.145	0.111	-0.388	0.139	-0.792	-1.138	0.199
<i>Alstonia boonei</i>	0.602	Small	0.421	1.037	0.671	-2.085	1.095	0.793	1.952	1.509	-4.108
		Large	-0.922	0.187	-1.163	1.448	0.458	-0.053	1.755	-0.634	0.003
<i>Amphimas pterocarpoides</i>	0.789	Small	1.282	1.765	-0.340	-0.708	-3.078	-1.252	0.319	-2.853	0.100
		Large	-0.203	0.467	-0.055	2.052	0.236	-0.057	-3.298	1.240	-0.037
<i>Anogeissus leiocarpa</i>	0.573	Small	-1.783	3.504	-0.962	-0.738	1.195	-0.109	-0.607	0.305	-0.849
		Large	-0.122	3.397	-0.836	0.789	0.504	-0.050	-2.110	0.735	-0.021
<i>Anopyxis klaineana</i>	0.62	Small	1.679	0.144	-0.105	-0.978	-0.343	-2.381	0.551	-1.240	-2.027
		Large	0.214	0.335	-0.827	-1.577	2.124	-0.123	0.909	0.312	-0.046
<i>Anthoantha macrophylla</i>	0.929	Small	1.468	11.366	-1.359	1.299	8.515	-0.915	-0.757	-1.941	-19.899
		Large	-0.149	0.165	1.164	-1.229	0.305	1.194	0.002	-0.677	1.231

<i>Anthostema aubryanum</i>	0.655	Small	0.240	3.094	0.440	1.647	-2.497	1.293	0.717	-0.199	0.905
		Large	0.684	0.095	-0.034	0.764	0.045	-0.009	-0.487	-0.264	-0.746
<i>Antiaris toxicaria</i>	0.535	Small	3.058	1.057	-0.187	-3.728	3.686	-0.240	-1.511	1.702	-0.321
		Large	0.266	1.201	-0.151	-9.026	4.200	-0.144	0.962	-0.978	0.040
<i>Antrocaryon micraster</i>	0.675	Small	0.447	0.092	2.242	-2.857	-0.127	2.462	-2.671	1.619	0.573
		Large	1.039	2.906	-7.371	2.716	2.626	-0.234	-2.340	3.338	-0.193
<i>Beilschmiedia mannii</i>	0.963	Small	3.254	0.148	0.407	-0.166	0.149	0.568	-0.216	-4.247	-3.634
		Large	-0.412	0.116	-0.559	-0.430	-0.019	0.026	-1.312	-0.822	0.092
<i>Berlinia confusa</i>	0.686	Small	2.777	5.832	-1.045	0.224	2.819	-0.453	0.048	4.512	-4.720
		Large	0.300	0.259	0.505	0.067	1.114	0.466	-2.670	1.288	0.498
<i>Bombax buonopozense</i>	0.538	Small	0.972	0.982	-0.191	-0.312	7.745	-3.403	-4.727	2.580	-0.185
		Large	-0.429	-0.547	-0.212	0.998	-0.505	0.017	-1.280	-0.475	0.054
<i>Buchholzia coriacea</i>	0.985	Small	2.504	0.389	0.863	-0.041	-0.716	1.169	-2.891	1.539	0.462
		Large	1.049	1.234	-0.095	0.218	0.778	-0.009	-1.257	-0.882	0.103
<i>Bussea occidentalis</i>	0.795	Small	6.961	-4.599	0.737	4.960	-5.645	1.032	5.509	-5.626	-2.100
		Large	0.462	-1.501	0.475	1.430	-1.660	0.490	-1.644	-2.934	0.608
<i>Calpocalyx brevibracteatus</i>	0.917	Small	2.674	-3.211	2.895	-0.342	-3.249	3.060	2.518	-6.811	-1.256
		Large	0.381	-1.836	-0.920	0.625	0.137	-0.015	0.243	-1.149	0.062
<i>Canarium schweinfurthii</i>	0.528	Small	0.198	2.179	-0.230	-0.523	0.159	0.134	4.062	-5.130	-1.096
		Large	-0.766	0.971	-0.706	0.330	0.943	-0.081	-0.620	0.357	-0.027
<i>Carapa procera</i>	0.979	Small	1.092	1.773	-0.329	1.054	-0.316	-4.580	1.933	-1.494	-0.711
		Large	0.814	1.201	-0.085	1.871	0.646	-0.044	0.591	-1.273	0.061
<i>Ceiba pentandra</i>	0.557	Small	3.669	2.441	1.117	0.883	2.539	1.291	0.029	-0.896	-2.382

		Large	0.183	0.542	-0.077	2.397	0.047	-0.043	-0.321	0.207	-0.016
<i>Celtis adolfi-friderici</i>	0.711	Small	1.867	2.280	-0.481	0.703	-0.015	-1.128	1.983	-1.615	-0.913
		Large	0.913	0.868	-0.361	-1.122	1.217	-0.058	-0.945	0.080	0.011
<i>Chidlowia sanguinea</i>	0.969	Small	0.768	1.665	0.030	-0.760	-0.471	0.415	-0.780	1.846	-0.514
		Large	-1.875	-0.127	1.184	-2.214	-0.338	1.202	-0.208	-1.025	1.170
<i>Chrysophyllum perpulchrum</i>	0.787	Small	0.688	0.801	-0.061	-0.340	-1.970	0.423	1.470	0.017	-5.102
		Large	1.092	1.203	-0.129	-0.336	1.268	-0.072	-1.950	-0.803	-0.890
<i>Chrysophyllum pruniforme</i>	0.653	Small	2.529	-0.972	3.617	-1.423	-2.148	4.070	5.957	-1.849	-0.024
		Large	-0.725	-1.197	0.048	-0.930	1.475	-0.087	-0.522	0.063	-0.007
<i>Cleistopholis patens</i>	0.674	Small	2.188	1.318	0.447	-1.063	-1.500	1.143	0.911	0.110	0.655
		Large	-3.210	0.766	1.158	-0.463	-0.286	1.212	-1.994	-0.483	1.238
<i>Coelocaryon oxycarpum</i>	0.793	Small	6.394	4.061	-0.713	0.432	5.984	-0.667	-3.033	-5.093	0.876
		Large	0.095	0.377	-0.175	0.948	-1.458	0.160	-1.014	-2.081	0.230
<i>Copaifera salikounda</i>	0.894	Small	3.622	0.072	0.389	0.339	0.103	0.559	0.354	-1.413	-0.936
		Large	0.940	-1.894	-2.031	1.317	0.925	-0.093	-1.844	1.355	-0.074
<i>Corynanthe pachyceras</i>	0.964	Small	2.402	0.380	-0.153	0.069	-3.691	0.596	-0.756	-0.993	-1.645
		Large	1.857	1.292	0.941	-0.682	2.000	0.943	-0.860	0.272	-0.189
<i>Coula edulis</i>	0.843	Small	2.012	1.800	0.117	-3.129	1.375	0.429	6.610	-5.941	-10.897
		Large	0.931	0.534	-0.066	-1.240	1.095	-0.044	-0.499	-1.619	0.100
<i>Cylicodiscus gabunensis</i>	0.553	Small	1.343	-0.289	0.283	-2.779	0.616	0.339	0.802	-0.891	-0.599
		Large	0.679	-0.364	-0.038	-0.446	1.009	-0.056	-0.076	-0.453	0.026
<i>Cynometra ananta</i>	0.577	Small	2.083	-0.448	1.602	-0.131	-0.480	1.701	-2.537	-0.341	0.665
		Large	1.265	0.291	-2.380	-0.014	2.463	-0.157	-0.525	1.893	-0.106

<i>Dacryodes klaineana</i>	0.842	Small	3.020	-1.854	0.803	-1.917	-0.518	0.812	0.555	-2.054	0.732
		Large	0.230	0.116	-1.222	0.337	0.355	-0.018	1.028	-0.447	0.015
<i>Dialium aubrevillei</i>	0.779	Small	4.737	-0.747	-0.128	0.463	-3.584	0.575	1.547	-2.709	-3.043
		Large	1.350	-0.569	-1.673	1.457	0.841	-0.077	-1.093	0.896	-0.042
<i>Dichapetalum guineense</i>	0.964	Small	6.560	-0.909	-0.178	1.333	-0.411	-3.518	-2.703	-4.871	0.735
		Large	-0.591	0.263	1.016	-1.225	0.078	1.048	-0.041	1.052	-0.364
<i>Discoglyprena caloneura</i>	0.831	Small	-0.603	-1.835	3.083	-2.488	-1.848	3.204	1.039	-0.392	-1.852
		Large	-0.009	0.046	-2.583	-1.462	1.441	-0.075	-2.315	0.615	-0.010
<i>Distemonanthus benthamianus</i>	0.65	Small	2.353	0.291	0.023	-1.660	1.359	0.072	1.107	-1.669	-0.497
		Large	0.635	0.348	-0.117	-0.500	-0.007	0.008	0.385	-0.745	0.036
<i>Duboscia viridiflora</i>	0.587	Small	3.620	0.001	-0.226	-1.063	-0.454	-2.635	0.786	0.369	-4.131
		Large	1.082	-0.113	-0.061	1.040	0.292	-0.045	-0.054	-0.537	0.026
<i>Entandrophragma angolense</i>	0.704	Small	2.302	4.676	1.232	-11.419	13.660	0.493	11.807	0.747	-3.227
		Large	-0.705	-0.143	0.195	-0.197	0.656	0.152	0.690	-0.667	0.220
<i>Entandrophragma cylindricum</i>	0.65	Small	1.259	-6.009	3.674	-6.561	-1.707	3.383	-4.928	1.351	2.052
		Large	-1.871	0.623	0.291	0.874	-0.166	0.319	-3.437	0.270	0.357
<i>Entandrophragma utile</i>	0.663	Small	1.679	-1.282	0.744	-1.614	-1.794	1.060	-2.269	-0.092	0.057
		Large	2.874	-0.668	-0.028	-0.276	1.052	-0.072	-1.466	-2.171	0.130
<i>Erythroxylum mannii</i>	0.634	Small	0.197	3.027	-0.434	1.091	0.089	0.003	1.872	2.426	-8.425
		Large	0.454	-1.541	-1.145	1.243	0.421	-0.044	-1.508	0.325	0.007
<i>Gilbertiodendron limba</i>	0.769	Small	2.541	0.110	0.154	-3.386	1.400	0.252	-0.913	-1.101	0.474
		Large	0.095	-0.871	0.026	-0.982	1.098	-0.059	1.158	-1.047	0.048
<i>Guarea cedrata</i>	0.828	Small	1.909	2.100	0.499	1.401	-0.054	0.875	-1.188	-0.689	-3.690

		Large	-1.239	-1.361	-0.496	0.163	0.862	-0.056	0.136	-0.145	0.005
<i>Guarea thompsonii</i>	0.861	Small	1.652	1.109	0.003	1.929	-0.599	0.259	-1.456	1.117	0.113
		Large	1.540	1.140	-5.636	-1.238	1.133	-0.061	-2.380	-1.616	0.118
<i>Guibourtia ehie</i>	0.589	Small	0.160	2.431	3.460	-1.234	0.945	3.808	-15.803	16.299	-1.623
		Large	2.859	-1.794	-2.476	3.294	0.802	-0.136	-0.917	0.698	-0.040
<i>Hannoa klaineana</i>	0.811	Small	0.176	2.226	-0.355	-0.212	-0.616	-0.740	-1.542	0.727	-0.249
		Large	1.541	0.336	-1.793	-0.822	1.542	-0.095	-0.301	0.400	-0.031
<i>Heritiera utilis</i>	0.637	Small	0.255	-0.312	0.904	1.052	-0.495	0.019	1.041	-0.091	-0.088
		Large	-0.027	0.814	-0.109	-0.420	0.859	-0.060	0.998	-1.029	0.047
<i>Hexalobus crispiflorus</i>	0.831	Small	3.126	0.460	-0.251	9.679	-5.361	-8.023	2.469	-0.153	-5.847
		Large	-2.561	1.764	-0.097	2.699	-0.168	-0.023	-4.125	-0.789	-0.097
<i>Holarrhena floribunda</i>	0.646	Small	1.494	-1.927	0.445	0.330	-1.002	0.300	1.163	1.059	-2.134
		Large	0.678	-3.247	-0.109	-0.613	0.404	-0.015	-0.415	-0.196	0.018
<i>Holoptelea grandis</i>	0.527	Small	1.097	0.320	0.485	0.112	-0.291	0.655	-1.776	-0.103	0.610
		Large	-0.138	-0.382	-0.496	-0.622	0.855	-0.058	1.202	0.202	-0.055
<i>Homalium letestui</i>	0.586	Small	1.736	1.574	0.565	-1.218	1.636	0.719	1.695	-0.357	0.021
		Large	-1.115	0.599	-0.048	0.589	0.891	-0.077	-0.440	0.382	-0.023
<i>Irvingia gabonensis</i>	0.72	Small	2.744	-0.971	10.768	-0.390	-1.755	11.057	9.780	3.984	-30.019
		Large	1.452	1.121	-1.217	0.316	1.616	-0.118	0.523	0.758	-0.069
<i>Khaya ivorensis</i>	0.614	Small	-0.847	2.914	-0.214	-0.865	1.177	0.053	-0.873	-0.729	0.061
		Large	-0.453	0.854	-0.073	-1.011	1.946	-0.110	-1.155	1.371	-0.077
<i>Klainedoxa gabonensis</i>	0.59	Small	6.077	-0.095	-0.345	-1.917	-0.387	-2.373	-2.111	4.714	-5.589
		Large	0.696	-0.672	-0.001	-1.639	1.067	-0.048	-2.154	0.600	-0.011

<i>Lananea welwitschii</i>	0.577	Small	-1.034	-0.008	0.789	-0.996	-1.531	1.043	0.296	0.522	-2.137
		Large	0.070	0.281	0.980	-0.846	0.477	1.008	-0.570	-0.298	1.047
<i>Leptaulus daphnoides</i>	0.99	Small	0.621	1.869	-0.294	-0.433	0.009	-0.673	-2.326	0.791	-0.024
		Large	-1.995	1.063	-0.063	-2.206	1.366	-0.052	0.328	0.244	-0.116
<i>Lonchocarpus sericeus</i>	0.794	Small	5.179	0.221	-0.352	0.975	-0.291	-6.797	-0.169	2.532	-1.395
		Large	0.752	-0.228	-0.013	0.996	0.279	-0.029	-0.972	0.166	-0.185
<i>Lophira alata</i>	0.762	Small	1.039	-1.417	1.522	-0.811	-0.228	1.301	-1.586	0.312	1.214
		Large	-0.673	0.259	-0.002	0.267	0.225	-0.004	1.119	-0.663	-0.199
<i>Lovoa trichilioides</i>	0.581	Small	0.747	3.856	-0.612	1.119	-0.866	0.140	-2.201	1.091	0.008
		Large	0.400	-0.318	-0.321	-1.476	1.452	-0.075	-0.967	0.242	-0.007
<i>Mammea africana</i>	0.759	Small	3.449	-0.089	0.424	-0.898	0.055	0.600	-5.744	0.051	-0.269
		Large	4.106	3.780	-0.545	2.740	-0.320	-0.023	-7.175	1.513	0.009
<i>Mansonia altissima</i>	0.532	Small	0.848	28.965	6.125	-8.446	34.580	5.711	27.246	2.451	-42.412
		Large	0.717	-0.001	0.306	-0.765	1.350	0.258	-0.174	0.441	0.305
<i>Margaritaria discoidea</i>	0.861	Small	1.420	0.866	-0.076	-6.451	4.675	-0.241	0.442	1.676	-0.466
		Large	-0.689	1.735	-0.130	1.948	0.691	-0.071	-3.146	-0.840	-2.346
<i>Millettia rhodantha</i>	0.86	Small	3.039	-1.226	5.015	-0.650	-1.349	5.209	-0.411	-1.805	-2.486
		Large	-0.471	-0.592	0.030	-0.626	1.145	-0.055	0.886	0.472	-0.059
<i>Monodora myristica</i>	0.962	Small	1.450	1.229	-0.230	-1.123	0.679	-0.065	-4.039	-1.729	0.188
		Large	1.019	0.271	0.473	-0.431	0.873	0.468	-1.790	0.901	0.202
<i>Morus mesozygia</i>	0.797	Small	3.074	0.001	-0.156	3.680	0.178	-8.829	-0.172	-1.260	-4.162
		Large	-0.146	-0.043	-0.024	-0.101	0.641	-0.028	0.086	0.014	0.003
<i>Musanga cecropioides</i>	0.726	Small	0.040	2.025	-0.270	1.194	-0.287	0.065	0.681	0.037	-0.129

		Large	0.940	0.154	-0.039	0.026	0.988	-0.047	-0.456	0.387	-0.020
<i>Myrianthus arboreus</i>	0.966	Small	1.420	1.506	0.031	-2.392	1.680	0.210	-1.565	0.177	-2.694
		Large	1.575	-0.256	0.634	-0.984	0.716	0.618	0.614	-2.647	0.811
<i>Nauclea diderrichii</i>	0.499	Small	2.818	-0.666	0.028	-21.561	13.611	-0.917	-2.369	1.069	-0.051
		Large	-2.142	-1.063	0.058	-0.172	0.552	-0.043	-1.672	-1.095	0.079
<i>Nesogordonia papaverifera</i>	0.607	Small	0.065	1.280	0.358	1.400	-1.400	0.732	-1.088	-2.992	1.020
		Large	-3.902	-0.556	0.052	-0.415	0.872	-0.050	-1.647	0.398	-0.002
<i>Ongokea gore</i>	0.538	Small	-0.743	2.118	-0.222	2.107	-0.764	-0.008	-0.088	0.058	-0.032
		Large	1.030	0.042	-2.031	-0.199	0.703	-0.047	-1.107	-0.130	0.020
<i>Pachypodanthium staudtii</i>	0.82	Small	3.955	0.039	-0.220	-0.464	-2.471	-3.254	0.812	2.772	-1.607
		Large	0.506	0.862	-0.094	-0.605	1.508	-0.096	-0.358	0.281	-0.018
<i>Panda oleosa</i>	0.92	Small	12.363	-5.442	0.207	1.338	27.957	-30.330	-9.318	30.747	-8.457
		Large	-0.121	0.648	0.303	0.468	0.805	0.297	-0.479	0.468	0.318
<i>Parinari excelsa</i>	0.732	Small	2.546	1.602	-0.371	-1.385	-1.454	-2.949	1.518	0.729	-1.346
		Large	-0.352	-1.036	-0.008	3.177	0.071	-0.054	0.212	0.284	-0.024
<i>Parkia bicolor</i>	0.602	Small	1.027	0.579	2.533	-1.421	0.462	2.645	-5.995	-4.584	-0.269
		Large	1.062	0.631	-0.709	0.260	1.625	-0.112	0.313	0.671	-0.055
<i>Pentaclethra macrophylla</i>	0.757	Small	2.899	-4.849	4.027	-1.003	-5.562	4.351	-1.032	-0.888	-0.490
		Large	2.579	1.202	-0.107	-1.798	2.923	-0.136	-0.067	3.250	-0.570
<i>Pentadesma butyracea</i>	0.709	Small	-2.142	-2.668	3.934	6.645	1.662	-0.107	1.520	-2.867	1.139
		Large	0.390	-1.198	0.595	-0.183	-0.520	0.577	0.036	-1.461	0.636
<i>Petersianthus macrocarpus</i>	0.614	Small	1.268	-0.344	0.299	-0.174	-1.169	0.483	-0.267	0.481	-0.127
		Large	-1.700	1.258	1.564	-0.301	1.066	1.575	0.964	-0.459	1.645

<i>Rhodognaphalon brevicuspe</i>	0.532	Small	1.459	2.762	-0.539	-1.149	1.119	-2.113	-2.241	1.432	-2.909
		Large	0.338	0.161	-0.157	-0.700	0.565	-0.035	-0.231	-0.792	0.042
<i>Phyllocosmus sessiliflorus</i>	0.846	Small	3.935	-4.623	6.465	0.913	-4.606	6.631	-4.438	-8.292	6.000
		Large	-4.353	0.708	1.764	0.459	-0.606	1.786	-0.433	-1.251	1.833
<i>Piptadeniastrum africanum</i>	0.551	Small	2.021	-1.462	1.586	-0.948	-1.439	1.754	0.918	6.713	-4.155
		Large	-0.450	1.051	-0.201	0.983	1.036	-0.091	-0.162	0.388	-0.032
<i>Protomegabaria stapfiana</i>	0.931	Small	1.107	1.838	-0.292	1.390	0.282	-2.831	-1.125	-0.487	-0.357
		Large	0.491	0.089	5.226	0.055	0.154	5.244	-2.769	-1.512	-3.096
<i>Pterygota macrocarpa</i>	0.548	Small	2.087	4.326	2.362	1.518	3.083	2.595	2.899	-8.658	-5.286
		Large	-1.346	0.342	0.820	-0.671	1.029	0.780	0.092	-0.240	0.850
<i>Pycnanthus angolensis</i>	0.563	Small	0.474	2.352	0.053	-1.209	1.521	0.265	0.520	-4.097	0.934
		Large	0.097	0.361	-0.070	1.569	0.517	-0.071	-0.468	0.954	-0.081
<i>Ricinodendron heudelotii</i>	0.707	Small	2.537	0.414	-0.185	-0.582	-1.775	0.378	-0.309	-2.443	-2.019
		Large	0.441	-0.630	-0.064	-1.134	0.689	-0.017	0.027	-1.077	0.060
<i>Sacoglottis gabonensis</i>	0.675	Small	-1.044	5.169	1.061	1.885	0.363	1.757	-0.303	-3.627	2.419
		Large	-1.746	0.900	0.920	0.837	0.297	0.931	-1.082	-0.168	0.979
<i>Scottellia klaineana</i>	0.852	Small	1.956	1.706	-0.073	-2.040	1.883	0.105	-1.572	-1.748	-1.648
		Large	-1.681	0.454	2.005	2.072	-0.379	2.011	-4.984	1.418	2.001
<i>Scytopetalum tieghemii</i>	0.89	Small	-0.242	2.198	-0.304	2.168	-1.057	-1.988	9.081	-5.126	-1.768
		Large	-0.839	3.063	0.845	-4.002	4.373	0.817	-3.556	1.257	0.986
<i>Spondianthus preussii</i>	0.818	Small	-1.208	1.217	-0.034	-0.380	2.674	-1.782	0.188	1.799	-1.712
		Large	-1.822	2.037	0.295	0.128	1.290	0.334	-1.952	1.194	0.361
<i>Sterculia oblonga</i>	0.602	Small	-6.062	2.262	3.101	-11.536	4.063	3.118	-0.930	2.791	0.488

		Large	0.807	-0.902	-1.450	2.215	-0.386	-0.018	-2.296	-1.455	0.116
<i>Sterculia rhinopetala</i>	0.675	Small	1.755	0.996	-0.261	-1.972	0.768	-0.008	2.216	-2.171	-2.070
		Large	-1.387	-1.947	-1.885	0.494	0.555	-0.038	0.676	-0.531	0.025
<i>Sterculia tragacantha</i>	0.727	Small	-0.247	0.479	1.101	-0.429	-0.621	1.285	-1.131	2.578	0.362
		Large	1.514	-0.583	0.000	1.597	1.097	-0.089	2.019	0.302	-0.055
<i>Stereospermum acuminatissimum</i>	0.803	Small	0.070	-0.641	0.499	-1.257	0.097	0.416	-0.528	-2.136	0.740
		Large	-1.087	1.354	-0.137	0.354	-0.049	0.015	1.365	-2.427	0.145
<i>Strephonema pseudocola</i>	0.88	Small	1.719	2.413	-0.460	1.159	0.491	-2.347	-1.098	-0.834	0.090
		Large	-0.635	0.530	-0.006	0.148	0.537	-0.002	0.560	-0.402	0.041
<i>Strombosia glaucescens</i>	0.882	Small	-0.397	2.759	-0.396	0.054	0.784	-0.143	-0.323	-1.507	-0.469
		Large	-6.299	5.378	-1.510	-2.465	1.740	-0.083	-1.088	0.085	0.004
<i>Terminalia ivorensis</i>	0.494	Small	0.499	1.602	-0.222	-1.077	-1.351	0.394	-2.081	-0.252	-1.764
		Large	0.829	0.484	-0.091	-1.518	1.189	-0.062	-1.849	0.478	-0.010
<i>Terminalia superba</i>	0.41	Small	2.019	-0.104	-0.006	-0.003	-1.077	0.314	-0.075	-0.492	-1.713
		Large	0.229	1.602	-0.246	1.069	1.529	-0.159	1.912	-1.386	0.045
<i>Tetrapleura tetraptera</i>	0.877	Small	-0.311	1.909	-0.311	-0.005	1.456	-0.414	-0.628	-0.736	0.053
		Large	2.572	-0.367	0.374	-0.201	0.372	0.394	0.483	-0.512	0.427
<i>Tieghemella heckelii</i>	0.752	Small	2.542	1.103	0.000	1.156	-0.528	0.336	1.304	-0.268	-1.646
		Large	-0.025	-0.096	-0.199	0.239	0.963	-0.070	0.382	-0.067	-0.012
<i>Treculia africana</i>	0.785	Small	3.704	-0.707	-0.073	0.768	-4.038	-0.080	-1.714	-0.090	-0.163
		Large	-0.967	-0.672	-1.173	0.889	-0.017	-0.003	0.371	-0.975	0.047
<i>Trichilia martineau</i>	0.954	Small	-0.305	0.079	0.552	0.518	-2.500	0.902	-3.344	1.395	-0.115
		Large	1.616	0.610	0.247	0.246	1.140	0.245	1.426	-0.787	-4.203

<i>Trichilia prieureana</i>	0.967	Small	4.029	0.042	-0.198	-0.075	2.762	-3.288	-1.802	1.555	-0.197
		Large	0.203	1.363	0.047	0.361	1.208	0.067	-1.684	0.606	0.117
<i>Trichilia tessmannii</i>	0.768	Small	1.580	1.661	-0.363	-2.196	2.546	-0.299	-4.248	-3.073	-0.192
		Large	-1.277	-1.309	0.031	-0.471	0.954	-0.053	-0.781	0.204	-0.005
<i>Trilepisium madagascariense</i>	0.753	Small	-0.902	0.126	2.122	-1.966	-1.045	2.354	-0.373	-2.535	1.075
		Large	2.132	0.254	-1.356	-1.841	1.307	-0.050	0.256	-0.112	-0.007
<i>Triplochiton scleroxylon</i>	0.442	Small	2.448	1.714	0.579	2.326	-0.009	0.886	-3.015	-1.227	1.226
		Large	-0.447	-0.225	-0.271	1.414	-0.158	-0.013	-0.768	-0.180	0.023
<i>Turraeanthus africanus</i>	0.841	Small	1.119	3.307	1.207	-0.886	1.982	1.542	-0.161	2.962	0.468
		Large	1.020	0.489	0.360	-1.764	0.752	0.429	-2.589	0.296	0.457
<i>Xylia evansii</i>	0.746	Small	-1.281	1.331	1.968	-2.677	2.255	1.805	0.967	-0.745	2.053
		Large	0.184	-1.174	0.634	0.761	-1.072	0.632	-1.017	-0.715	0.628
<i>Xylopia staudtii</i>	0.838	Small	2.604	0.349	-0.183	-2.645	-0.261	-1.831	0.858	1.536	-4.162
		Large	-1.030	-0.890	-1.719	-0.028	1.328	-0.102	-0.486	0.939	-0.064
<i>Zanthoxylum gilletii</i>	0.697	Small	2.410	0.449	0.215	-0.590	0.247	0.470	2.891	-1.696	0.268
		Large	-0.148	-0.370	-2.192	2.565	0.053	-0.050	1.843	-0.987	0.033

Appendix 3. Phylogeny for the tree species (Webb & Donoghue 2003, revision R20030804).

AGP-0	AGP-1	AGP-2	Order	SubOrder	family	Tribe	Name
Highest rank	Second rank	3rdrank					
Eudicots	Asterids	Ericales	Ericales	Ericales	Lecythidaceae	Lecythidaceae	<i>Petersianthus macrocarpus</i>
Eudicots	Asterids	Ericales	Ericales	Ericales	Lecythidaceae	Scytopetalaceae	<i>Scytopetalum tieghemii</i>
Eudicots	Asterids	Ericales	Ericales	Ericales	Sapotaceae	Sapotaceae	<i>Chrysophyllum perpulchrum</i>
Eudicots	Asterids	Ericales	Ericales	Ericales	Sapotaceae	Sapotaceae	<i>Chrysophyllum pruniforme</i>
Eudicots	Asterids	Ericales	Ericales	Ericales	Sapotaceae	Sapotaceae	<i>Synsepalum afzelii</i>
Eudicots	Asterids	Ericales	Ericales	Ericales	Sapotaceae	Sapotaceae	<i>Tieghemella heckelii</i>
Eudicots	Asterids	Euasterid-1	8PP	Gentianales	Apocynaceae	Apocynoideae	<i>Holarrhena floribunda</i>
Eudicots	Asterids	Euasterid-1	8PP	Gentianales	Apocynaceae	Rauvolfioideae	<i>Alstonia boonei</i>
Eudicots	Asterids	Euasterid-1	8PP	Lamiales	Bignoniaceae	Bignoniaceae	<i>Stereospermum acuminatissimum</i>
Eudicots	Asterids	Euasterid-1	8PP	Rubiaceae	Rubiaceae	Cinchonoideae	<i>Corynanthe pachyceras</i>
Eudicots	Asterids	Euasterid-1	8PP	Rubiaceae	Rubiaceae	Cinchonoideae	<i>Nauclea diderrichii</i>
Eudicots	Asterids	Euasterid-1	Icacinaceae	Icacinaceae	Icacinaceae	Icacinaceae	<i>Leptaulus daphnoides</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	DetarieaeSL	DetarieaeSS	<i>Anthonotha macrophylla</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	DetarieaeSL	DetarieaeSS	<i>Berlinia confusa</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	DetarieaeSL	DetarieaeSS	<i>Copaifera salikounda</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	DetarieaeSL	DetarieaeSS	<i>Cynometra ananta</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	DetarieaeSL	DetarieaeSS	<i>Gilbertiodendron limba</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	DetarieaeSL	DetarieaeSS	<i>Guibourtia ehie</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Dialiinae	Dialiinae	<i>Dialium aubrevillei</i>

Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Caesalpinieae	<i>Bussea occidentalis</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Caesalpinieae	<i>Chidlowia sanguinea</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Cassieae	<i>Distemonanthus benthamianus</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Ingeae	<i>Albizia adianthifolia</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Ingeae	<i>Albizia zygia</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Mimoseae	<i>Calpocalyx brevibracteatus</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Mimoseae	<i>Cylicodiscus gabunensis</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Mimoseae	<i>Piptadeniastrum africanum</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Mimoseae	<i>Tetrapleura tetraptera</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Mimoseae	<i>Xylia evansii</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Parkieae	<i>Parkia bicolor</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Mimosoideae	Parkieae	<i>Pentaclethra macrophylla</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Papilionoideae	Millettieae	<i>Lonchocarpus sericeus</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Papilionoideae	Millettieae	<i>Millettia rhodantha</i>
Eudicots	Rosids	Eurosid-1	Fabales	Fabaceae	Papilionoideae	Sophoreae	<i>Amphimas pterocarpoides</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	03AA	Erythroxylaceae	Erythroxylaceae	<i>Erythroxylum mannii</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	03AA	Erythroxylaceae	Rhizophoraceae	<i>Anopyxis klaineana</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	03AA	Phyllanthaceae	Phyllanthaceae	<i>Margaritaria discoidea</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Achariaceae	Achariaceae	Achariaceae	<i>Scottellia klaineana</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Chry/Dich	Chrysobalanaceae	Chrysobalanaceae	<i>Parinari excelsa</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Chry/Dich	Dichapetalaceae	Dichapetalaceae	<i>Dichapetalum madagascariense</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Euphorbiaceae	Euphorbiaceae	Euphorbieae	<i>Anthostema aubryanum</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Euphorbiaceae	Euphorbiaceae	Euphorbieae	<i>Discoglyprena caloneura</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Euphorbiaceae	Euphorbiaceae	Euphorbieae	<i>Protomegabaria stapfiana</i>

Eudicots	Rosids	Eurosid-1	Malpighiales	Euphorbiaceae	Euphorbiaceae	Euphorbieae	<i>Ricinodendron heudelotii</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Euphorbiaceae	Euphorbiaceae	Euphorbieae	<i>Spondianthus preussii</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Flacouriales	Ixonanthaceae	Ixonanthaceae	<i>Phyllocosmus africanus</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Flacouriales	Salicaceae	Homalieae	<i>Homalium letestui</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Humiriaceae	Humiriaceae	Humiriaceae	<i>Sacoglottis gabonensis</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Irv-Clu	Clusiaceae	Clusiaceae	<i>Allanblackia floribunda</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Irv-Clu	Clusiaceae	Clusiaceae	<i>Mammea africana</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Irv-Clu	Clusiaceae	Clusiaceae	<i>Pentadesma butyracea</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Irv-Clu	Irvingiaceae	Irvingiaceae	<i>Irvingia gabonensis</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Irv-Clu	Irvingiaceae	Irvingiaceae	<i>Klainedoxa gabonensis</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Ochnaceae	Ochnaceae	Ochnaceae	<i>Lophira alata</i>
Eudicots	Rosids	Eurosid-1	Malpighiales	Pandaceae	Pandaceae	Pandaceae	<i>Panda oleosa</i>
Eudicots	Rosids	Eurosid-1	Rosales	Rosales	Cannabaceae	Cannabaceae	<i>Celtis adolfi-friderici</i>
Eudicots	Rosids	Eurosid-1	Rosales	Rosales	Moraceae	Moraceae	<i>Antiaris toxicaria</i>
Eudicots	Rosids	Eurosid-1	Rosales	Rosales	Moraceae	Moraceae	<i>Morus mesozygia</i>
Eudicots	Rosids	Eurosid-1	Rosales	Rosales	Moraceae	Moraceae	<i>Treculia africana</i>
Eudicots	Rosids	Eurosid-1	Rosales	Rosales	Moraceae	Moraceae	<i>Trilepisium madagascariense</i>
Eudicots	Rosids	Eurosid-1	Rosales	Rosales	Urticaceae	Cecropiaceae	<i>Musanga cecropioides</i>
Eudicots	Rosids	Eurosid-1	Rosales	Rosales	Urticaceae	Urticaceae	<i>Myrianthus arboreus</i>
Eudicots	Rosids	Eurosid-1	Rosales	Ulmaceae	Ulmaceae	Ulmaceae	<i>Holoptelea grandis</i>
Eudicots	Rosids	Eurosid-2	Brassicales	Brassicales	Brassicaceae	Brassicaceae	<i>Buchholzia coriacea</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Bombacoideae	<i>Bombax buonopozense</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Bombacoideae	<i>Ceiba pentandra</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Bombacoideae	<i>Rhodognaphalon brevicuspe</i>

Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Heritiera utilis</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Mansonia altissima</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Nesogordonia papaverifera</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Pterygota macrocarpa</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Sterculia oblonga</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Sterculia rhinopetala</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Sterculia tragacantha</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Sterculioideae	<i>Triplochiton scleroxylon</i>
Eudicots	Rosids	Eurosid-2	Malvales	Malvadendrina	Malvaceae	Tilioideae	<i>Duboscia viridiflora</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Anac/Burs	Anacardiaceae	Anacardiaceae	<i>Antrocaryon micraster</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Anac/Burs	Anacardiaceae	Anacardiaceae	<i>Lannea welwitschii</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Anac/Burs	Burseraceae	Burseraceae	<i>Canarium schweinfurthii</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Anac/Burs	Burseraceae	Burseraceae	<i>Dacryodes klaineana</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Carapeae	<i>Carapa procera</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Meliaceae	<i>Entandrophragma angolense</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Meliaceae	<i>Entandrophragma cylindricum</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Meliaceae	<i>Entandrophragma utile</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Meliaceae	<i>Guarea cedrata</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Meliaceae	<i>Guarea thompsonii</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Meliaceae	<i>Khaya ivorensis</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Meliaceae	<i>Lovoa trichilioides</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Trichilieae	<i>Trichilia martineauii</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Trichilieae	<i>Trichilia priureana</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Trichilieae	<i>Trichilia tessmannii</i>

Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Meliaceae	Turraeeae	<i>Turraeanthus africanus</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Rutaceae	Rutaceae	<i>Zanthoxylum gilletii</i>
Eudicots	Rosids	Eurosid-2	Sapindales	Meli/Ruta/Sim	Simaroubaceae	Simaroubaceae	<i>Hannoa klaineana</i>
Eudicots	Rosids	Myrtales	Myrtales	Combretaceae	Combretaceae	Combretoideae	<i>Anogeissus leiocarpa</i>
Eudicots	Rosids	Myrtales	Myrtales	Combretaceae	Combretaceae	Combretoideae	<i>Terminalia ivorensis</i>
Eudicots	Rosids	Myrtales	Myrtales	Combretaceae	Combretaceae	Combretoideae	<i>Terminalia superba</i>
Eudicots	Rosids	Myrtales	Myrtales	Combretaceae	Combretaceae	Strephonematoideae	<i>Strephonema pseudocola</i>
Eudicots	Santalales	Santalales	Santalales	Santalales	Olacaceae	Anacoloosoideae	<i>Strombosia glaucescens</i>
Eudicots	Santalales	Santalales	Santalales	Santalales	Olacaceae	Aptandrae	<i>Ongokea gore</i>
Eudicots	Santalales	Santalales	Santalales	Santalales	Olacaceae	Couleae	<i>Coula edulis</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Lauraceae	Lauraceae	<i>Beilschmiedia mannii</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Annonaceae	Annonaceae	<i>Cleistopholis patens</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Annonaceae	Annonaceae	<i>Duguetia staudtii</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Annonaceae	Annonaceae	<i>Hexalobus crispiflorus</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Annonaceae	Annonaceae	<i>Monodora myristica</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Annonaceae	Annonaceae	<i>Xylopia staudtii</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Myristicaceae	Myristicaceae	<i>Coelocaryon sphaerocarpum</i>
Magnoliids	Magnoliidae	Magnoliidae	Magnoliales	12I	Myristicaceae	Myristicaceae	<i>Pycnanthus angolensis</i>