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The contribution of interspecific variation in maximum tree height to tropical and temperate diversity

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Abstract: Maximum height was assessed for tree species from seven temperate deciduous forests, one subtropical forest and one tropical forest and combined with published tree heights for three other tropical forests. The temperate deciduous forests showed a strong concentration of canopy species and a dearth of subcanopy species. In contrast, the four tropical forests showed more uniform distributions of maximum heights, while the subtropical forest had an intermediate distribution. The tropical and subtropical sites had greater densities of small trees than did the temperate sites and most of these small trees were members of small- to medium-sized species. Sapling recruitment per unit stem basal area increased with declining maximum height in Panama, which is consistent with the criterion for coexistence of species of differing stature derived from Kohyama's forest architecture hypothesis. Greater penetration of light into gaps and favourable conditions for growth over most of the year may allow more smaller-statured species to coexist with canopy trees in tropical vs. temperate forests.

Key Words: Australia, biodiversity, forest architecture hypothesis, forest stratification, Panama, temperate forest, tree height, tropical forest, USA

INTRODUCTION

Tropical forest trees show great diversity in size (Kohyama 1996, Richards 1996, Turner 2001), with adult heights ranging from 1 to 40–70 m on sites without severe water or nutrient limitations. Understorey and subcanopy trees appear to be quite diverse among wet lowland forests of the neotropics (Pitman *et al.* 2002, Popma *et al.* 1988, Valencia *et al.* 2004). In contrast, the deciduous forests of eastern North America include some shrubs and understorey trees, but show greater concentrations of large-statured canopy trees and a dearth of subcanopy species (Pacala *et al.* 1996). The higher diversity of tropical vs. temperate forests has been associated with this greater diversity in adult stature, which may reflect reduced exclusion of smaller-statured species by canopy species at lower latitudes (Kohyama 1993, 1996).

Despite the importance of tree height in forest communities, there have been few quantitative studies of within-forest variation in the adult height of the constituent species. Earlier studies, summarized by Richards (1952) and Smith (1973), have described variation in tree stature in terms of forest stratification, reporting three to five strata of trees in wet tropical forests, as compared to two strata (understorey and overstorey) in temperate deciduous forests. Distinct concentrations of foliage at different heights may often be observed along any single vertical transect (Ashton & Hall 1992, Koike & Syahbuddin 1993). However, such distinctions are blurred when averaged over multiple vertical transects (Kira 1978, Parker & Brown 2000, Popma *et al.* 1988), and the co-occurrence of trees in all ontogenetic stages obscures the effects of interspecific differences in stature on forest strata (Richards 1996, Whitmore 1998). More recent classifications of species into four or five adult size categories on large-scale plots also indicate broad variation in stature within tropical forests (Condit *et al.* 1996, Kochummen *et al.* 1990), but these categories are approximations and include no measured heights of the constituent species. Thus, temperate and tropical forests differ in their distributions of adult stature, but the exact nature of these differences and their relation to diversity remain uncertain.

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Comprehensive measurements of tree height in seven temperate deciduous forests, one subtropical and one tropical forest were combined with reported height distributions for three other tropical forests to address the following questions:

(1) What are the quantitative differences in the distributions of maximum tree heights (h_{max}) among species between tall temperate deciduous forests of the USA and tropical forests?
(2) Do the relative abundances of adult understorey trees vs. juveniles of taller species differ between temperate and tropical forests?
(3) To what extent are differences in overall tree diversity among the sites associated with differences in the distribution of h_{max}?

In addition, we evaluated recruitment efficiency (defined as saplings recruited per unit basal area of larger conspecifics) and seed and seedling survival to assess possible mechanisms of coexistence of tree species of different adult stature. This definition of recruitment efficiency was chosen to test the forest architecture hypothesis of Kohyama (1993, 1996), which identifies sapling recruitment per unit basal area as a key variable in the coexistence of different-sized species.

METHODS

Sites and tree selection

Trees of temperate deciduous forests were measured in seven forests across the eastern, central and south-eastern sections of the USA (Table 1). The study sites included rare remnants of once widespread, old-growth forests, usually on moist, fertile soils of protected hollows, north-facing slopes or more level ground (Kershner & Leverett 2004, Martin 1975, McClain *et al.* 2001, Schmeltz *et al.* 1974, White & White 1996). The forests were all in the deciduous forest formation of Braun (1950), but varied greatly in species composition. The forests were entirely or predominantly deciduous, with the inclusion of one or two coniferous overstorey species at three sites and the large evergreen shrub, *Rhododendron maximum* L., at two sites. There were five upland forests and two bottomland forests (Illinois and North Carolina). Two stands of similar (north-facing) slope and species composition, separated by 7 km, were combined as a single site that included Ogle Hollow in Brown County State Park and the hollow to the south of Crooked Lake in Yellowwood State Forest, Indiana. Six mid-elevation cove forests (hollows or sheltered north- or east-facing slopes) located within 35 km of each other were combined as a single site in the Great Smoky Mountains National Park, Tennessee. The north-facing slope north-west of Todd Mountain was searched at Mohawk Trail State Forest, Massachusetts.

At each site, 2–5-d searches were made for the tallest individuals of every free-standing species attaining a height ≥ 4 m. All species were included for which relatively large, old individuals could be found. On the sites with substantial variation in elevation, searches were restricted to hollows and low to midslope positions, as trees grow taller in such sheltered positions than on upper slopes and ridges (McNab 1989). Only the floodplain areas were searched at Beall Woods, Illinois, as the adjacent upland forest had a different species composition (McClain *et al.* 2001).

Broad-leaved evergreen trees of a subtropical rain forest were measured on a 1.94-ha plot (Connell *et al.* 1984), plus additional trees were measured in a small adjacent area, in Lamington National Park, Queensland, Australia. A list of tree coordinates was used to find the largest diameter trees of the more common species. All 18 species with ≥ 15 tagged trees ≥ 10 cm dbh were measured, as were 15 of the 30 species with 4–14 tagged trees. For species seldom or never exceeding 10 cm dbh, we measured four of the eight species with ≥ 5 stems among the 2.5–10 cm dbh trees in the 0.59-ha area censused for saplings (Connell *et al.* 1984). The largest trees of each selected species generally had rounded crowns and relatively thick limbs indicating maturity or old age.

Table 1. Site descriptions based on United States Geological Survey (1970), Martin (1975), Schmeltz *et al.* (1974), Muller (1982), Connell *et al.* (1984) and Leigh (1999). Coordinates for Brown Co. and Great Smoky Mountains National Park are means for multiple stands. Temperate forest types (in USA) after Küchler (1964).

Site	Forest type	Location	Elevation (m)	Annual precip. (m)
Mohawk Trail State Forest, MA, USA	Northern hardwoods	42°39′N, 72°58′W	200–300	1.3
Brown, Co., IN, USA	Beech-maple	39°9′N, 86°16′W	200–250	1.1
Donaldson's Woods, IN, USA	Oak-hickory	38°44′N, 86°24′W	200	1.1
Beall Woods Nature Pres., IL, USA	Southern floodplain	38°23′N, 87°53′W	120	1.2
Lilley Cornett Woods, KY, USA	Mixed mesophytic	37°5′N, 83°0′W	320–500	1.3
Big Oak Woods, NC, USA	Oak-hickory-pine (bottomland)	35°53′N, 79°1′W	80	1.15
Great Smoky Mtns N.P., TN, USA	Mixed mesophytic (cove)	35°43′N, 83°24′W	800–1100	1.5+
Lamington N.P., Australia	Subtropical evergreen	28°14′S, 153°10′E	900	1.9
Gigante, Panama	Tropical lowland	9°6′N, 79°51′W	60	2.6

A set of 6256 height measurements was used to characterize the distribution of adult heights for a lowland tropical forest located on the Gigante Peninsula of the Barro Colorado Nature Monument, Panama. Tree heights were measured for individuals from a wide size range for 95 of the more common species. For each of these species, all individuals ≥ 10 and ≥ 1 cm dbh were measured within 36 nested subplots of 0.16 and 0.06 ha each, respectively. The nested subplots were spread uniformly over a 38.4-ha plot where all individuals ≥ 20 cm dbh were mapped and identified. Additional large trees were measured for the larger species over the entire 38.4-ha plot. The forest at this site is more than 200 y old.

The chosen sites were all relatively favourable for tree growth. The deciduous forest stands all receive substantial rain during the summer growing season, with a mean annual precipitation of 1.0 to 1.5 + m y^{-1} (Table 1) and a frost-free growing season of 140–210 d (Martin 1975, United States Geological Survey 1970). The subtropical forest site receives about 1.9 m y^{-1} of precipitation, with a summer rainfall maximum (Connell *et al.* 1984). Mean daily maximum and minimum temperatures for the warmest and coolest months for the nearest weather station at Mt Tamborine (525 m elevation) are respectively, 25.7 and 17.1 °C in January and 17.1 and 8.0 °C in July (http://www.bom.gov.au/climate/averages/tables/ca_qld_names.shtml). The tropical site receives about 2.6 m y^{-1} of rain with a 4-mo dry season, during which time some of the canopy trees lose their leaves, as described by Leigh (1999) for the nearby forest on Barro Colorado Island. Mean monthly temperatures are 27 °C in April and 26 °C in all other months (Leigh 1999).

Species diversity was characterized by Fisher's α, a measure which is relatively insensitive to plot size and shape (Leigh 1999). The measure was calculated for the four enumerated sites (Donaldson's Woods, Indiana; Lilley Cornett Woods, Kentucky; and the tropical and subtropical sites).

Height measurements

Tree heights on the subtropical and temperate sites were determined by first measuring the eye-to-leaf distance of the highest twigs or leaves with a calibrated optical or laser rangefinder and then multiplying that distance by the sine of the sighting angle to the horizontal (measured by clinometer). Similar methods were used to calculate the height of the sighting point above the tree base, which was then added to the eye-to-top height to yield the total height above the base. This technique is judged superior to the traditional method of estimating heights from horizontal distances and sighting angles, because the usual assumption that the highest visible point is directly above the base, albeit reasonable for young, conical trees, is questionable for spreading old trees.

At the tropical site, heights to 15 m were measured with a telescoping pole. Taller trees were measured from the tree base with a laser rangefinder, with tree height taken as observer height plus the greatest of multiple vertical reflections from the upper crown of the tree. The resulting plots of height vs. dbh were inspected to see if the tallest trees were outliers for each species. The more obvious outliers were remeasured, from which it was inferred that for a few of the hundreds of measurements of mature trees, heights were likely misrecorded by 10 m, or a branch of a taller, overarching tree was measured. Based on this inference, a few additional outlying heights were discarded. The number of species was also reduced to 85 by omitting 10 species with few trees in the upper halves of their diameter distributions.

Maximum height estimation

A number of methods have been used to estimate maximum height per species including asymptotic approaches (Thomas 1996) and the choice of the 95th percentile in height among all trees greater than 5 or 10 cm dbh (Kohyama *et al.* 2003, Poorter *et al.* 2003). As we lacked the necessary height distributions for such methods at most sites, we simply took the heights of the tallest trees per species, as direct measures of maximum height. However, a potential problem with this approach is that trees of greater heights are likely to be encountered among the commonest species. This bias was reduced by averaging the heights of the three tallest measured trees for the most common species, averaging the heights of the two tallest trees for species of intermediate abundance and using the greatest height recorded for less-abundant species. As the resulting maximum heights differed little from those derived by using the maximum measured height for every species, the approach was judged adequate for comparing different forest types.

To better assess height patterns in tropical forests, we included maximum heights of the 27 species measured by Kohyama *et al.* (2003) on two 1-ha plots in a lowland mixed dipterocarp forest of western Borneo and the 53 species measured by Poorter *et al.* (2003) on 20 1-ha plots in lowland evergreen moist forest of Liberia. The species included had ≥ 20 individuals ≥ 5 cm dbh on the Bornean plots and ≥ 10 individuals of 10–20 cm dbh and a maximum diameter ≥ 15 cm on the Liberian plots. We also included the inferred distribution of asymptotic maximum heights for the 50-ha plot at Pasoh Forest, Malaysia derived by Thomas (2003) from the diameter distributions of all species and a relation between asymptotic height and the 97th percentile of diameter of trees ≥ 1 cm dbh determined for 42 of these species. Of the species measured by Kohyama *et al.* (2003), 12/27 also occurred on the Pasoh plot. There was no overlap among the species sampled for Africa, South-East Asia, subtropical Australia, Central America and North America.

Sapling recruitment

Kohyama (1993) hypothesized that small-statured species require greater recruitment efficiency than do larger species to persist in tall forests, i.e. that recruitment per unit of basal area must be higher in small-statured species. This hypothesis was assessed at the tropical site, where sapling recruitment could be determined over a substantial, 2.16-ha area (the 36 0.06-ha plots where all trees $\geq$ 1 cm dbh were measured). For each species, the rate of recruitment per unit basal area was estimated using the method of Kohyama & Takada (1998). They estimated recruitment from sapling density in the size class centred on the recruitment size threshold and the mean growth rate for this size class. We used a sapling size class of 1–1.9 cm and a recruitment size threshold of 1.5 cm dbh. Thus, the sapling recruitment rate was estimated as $R = G \times f$, where G is the mean stem diameter growth rate (cm y^{-1}), f is the number of saplings per unit area and diameter class width (no. ha^{-1} cm^{-1}) for saplings of 1–1.9 cm dbh, and R is the estimated recruitment rate per unit area and time (no. ha^{-1} y^{-1}) into the $\geq$ 1.5 cm dbh size class. The mean value of G of 0.06 cm y^{-1} reported by Condit *et al.* (1999) for 1–1.9-cm-dbh saplings at Barro Colorado (BCI), Panama was used here with the observed species-specific values of f to calculate R. This recruitment rate was then divided by the basal area per ha of all conspecific stems $\geq$ 1.5 cm dbh to yield recruitment per unit basal area.

Seed and first-year seedling survival were assessed for small- vs. large-statured species using 200 stations located in a stratified random fashion within the 50-ha plot on BCI, which is 4 km from the Gigante plot. Each station included one 0.5-m^2 seed trap, constructed of 1-mm mesh screen, and three adjacent 1-m^2 seedling plots (see Wright *et al.* 2003 for detailed methodology). All seeds were identified and counted in weekly censuses conducted from 1 January 1987 through 31 December 2001. All woody plants $\leq$50 cm tall were tagged and identified between January and March 1994. Survivors were re-measured and new recruits were tagged and identified between January and March each year from 1995 to 2002. Seed survival (seedlings per seed) was estimated as the density of seedling recruits divided by the density of conspecific seeds for species with 10 or more seeds captured in the appropriate years. First-year seedling survival (% y^{-1}) was estimated as the proportion of new recruits that survived until the next annual census for species with 10 or more seedling recruits. Seed and seedling survival and seed mass were transformed logarithmically to normalize the residuals. The effect of tree stature on seed and seedling survival was then assessed using an analysis of covariance (ANCOVA), which treated survival as the dependent variable, tree stature as the grouping factor, and seed mass as the covariate. The grouping factor had two levels, which were understorey trees including shrubs and treelets vs. canopy trees including mid-sized and large trees as defined by Condit *et al.* (1996). Mean dry seed mass was for endosperm plus embryo for up to four seeds chosen at random from up to five randomly chosen fruits from up to five randomly chosen individuals of each species.

RESULTS

The temperate sites all showed strong concentrations of maximum height over a narrow range. Therefore we present numbers of species per quarter octave height range (Figure 1). Quarter octaves result in four geometrically or logarithmically equal divisions for every doubling in height. Geometric height classes were used because relative height may be more important than absolute height in determining the crown overlap of trees of differing heights. Of the 69 temperate species measured across all sites, 14 to 25 were measured on any one site. The temperate species were measured at an average of 2.0 of the seven temperate sites. Thus, our seven temperate forests are not repeated measures of the same forest, but rather are closer to being independent measures of temperate deciduous forest structure. The across-site coefficient of variation of conspecific h_{max} averaged 6.7% for the 31 species occurring at multiple sites. This small coefficient of variation of approximately one-third of the quarter octave height class range represents an upper bound on the random error in h_{max}, as it also reflects genetic and environmental differences between sites.

Striking differences in the distributions of maximum height among species were observed between the temperate deciduous sites and the subtropical and tropical sites (Figures 1 and 2). For each of the seven temperate sites, the majority of the measured species were in the largest height classes ($h_{max} \geq 28.3$ m), with a peak in the $33.6 < h_{max} < 40$ m class in every case (Figure 1). In contrast, few species were found in the next three smaller size classes ($16.8 < h_{max} < 28.3$ m). Henceforth, species with $h_{max} \geq 28.3$ m or with $16.8 < h_{max} < 28.3$ m will be referred to as canopy and subcanopy species, respectively. The subtropical and in particular, the tropical sites, showed more even distributions of species maximum heights (Figure 2). The temperate sites showed, on average, a 6 to 1 ratio of canopy to subcanopy species, while the tropical and subtropical sites had roughly

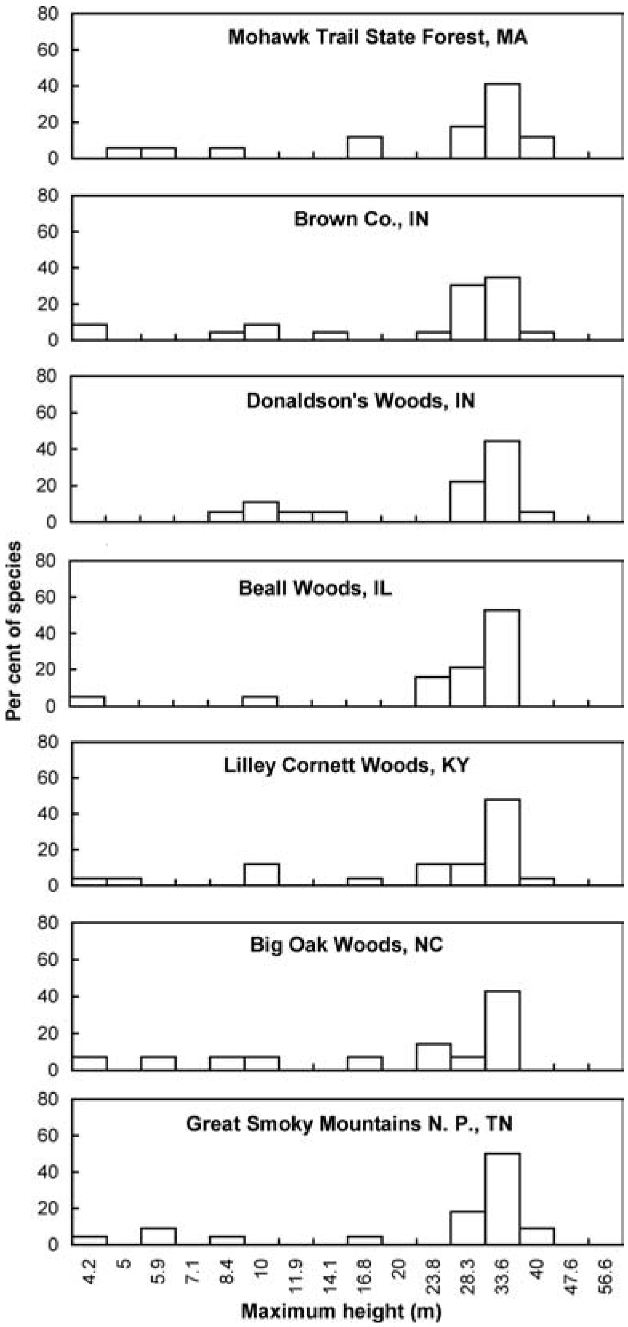

Figure 1. Distribution of maximum height per species for the temperate sites. Heights listed along the abscissa are lower limits of quarter octave height classes.

equal numbers of species in these two groups (Table 2). This dearth of subcanopy species in temperate forests is even more pronounced when the species are weighted by the number of trees per species (Figure 3, Table 2). Short understorey species are missing at the Bornean and African sites because maximum height was only determined for species exceeding ~10 or 15 cm dbh, respectively, in these forests.

The temperate and tropical sites also showed contrasting patterns in the abundance of small stems of large- vs. smaller-statured species (Table 3). Juveniles of canopy species dominated the 2.5–10 cm dbh and 10–20 dbh size classes of Lilley Cornett Woods and Donaldson's Woods, respectively, the two temperate sites for which this information was available. In contrast, the tropical and subtropical sites had much higher densities of total stems in these size classes, which were dominated by smaller species (Table 3).

The greater species diversity of the tropical and subtropical sites was mostly due to the high diversity of understorey and subcanopy species at these sites, relative to the temperate sites (Table 4). Although the tropical and subtropical sites had greater diversity among canopy species than did the temperate sites, the latitudinal difference in overall diversity was much augmented by the contrasting distributions of smaller species.

The larger temperate species showed a broad range in shade tolerance, as assessed by foresters, while no intolerant understorey species ($h_{max} < 16.8$ m) was measured (Figure 4). Published mortality rates for saplings under high canopy on BCI (Welden *et al.* 1991), 4 km from the Gigante site, indicate a broad range in shade tolerance over all adult size classes (Figure 4).

At the tropical site, the estimated recruitment rate per unit basal area for 1.5-cm-dbh saplings showed a strong negative correlation with h_{max} ($r = -0.80$). There was a 300-fold decline in recruitment efficiency over a 10-fold range in h_{max} (Figure 5).

This decline in sapling recruitment efficiency with increasing h_{max} was associated with significantly lower seed and seedling survival among large-statured canopy tree species vs. small-statured understorey tree species (Figures 6 and 7). *Jacaranda copaia* had unusually low seedling survival (2.6% compared with other species in Figure 7), was an extreme outlier from the ANCOVA

Table 2. The percentages (mean ± 1 SE) of species and of individual trees comprised of canopy ($h_{max} \geq 28.3$ m) vs. subcanopy species ($16.8 < h_{max} < 28.3$ m). Sample size is seven temperate, one subtropical, and four tropical sites for species and two temperate, one subtropical and one tropical site for individuals. Percentages for individuals only are restricted to plots enumerated for individuals ≥ 10 cm in diameter at breast height (Muller 1982, Schmeltz *et al.* 1974, this study).

	Percentage of species for which		Percentage of trees for which	
Region	$h_{max} \geq 28.3$ m	$16.8 < h_{max} < 28.3$ m	$h_{max} \geq 28.3$ m	$16.8 < h_{max} < 28.3$ m
Temperate deciduous	68 ± 3	11 ± 3	93 ± 6	3 ± 4
Subtropical	38	35	49	40
Tropical	35 ± 3	44 ± 5	38	57

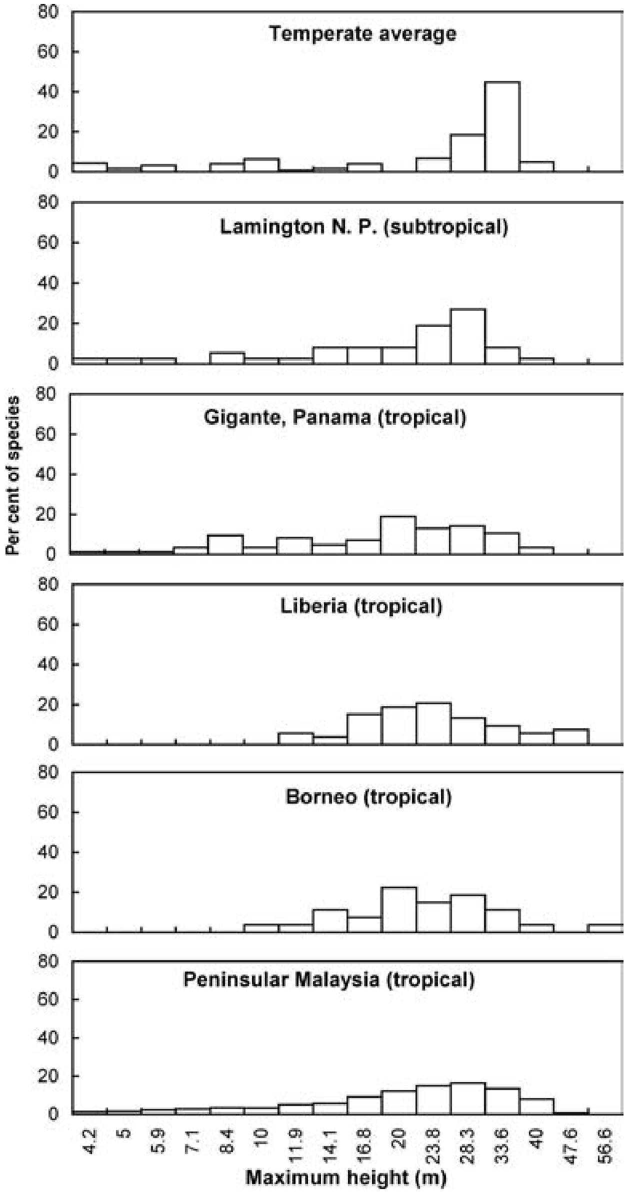

Figure 2. Distribution of maximum height per species for all regions, including forests measured by Poorter *et al.* (2003) in Liberia, Kohyama *et al.* (2003) in Borneo and Thomas (2003) in Peninsular Malaysia. The absence of short understorey species at the Bornean and Liberian sites reflects exclusion of species not attaining ~10 or 15 cm dbh, respectively. Heights listed along the abscissa are lower limits of quarter octave height classes.

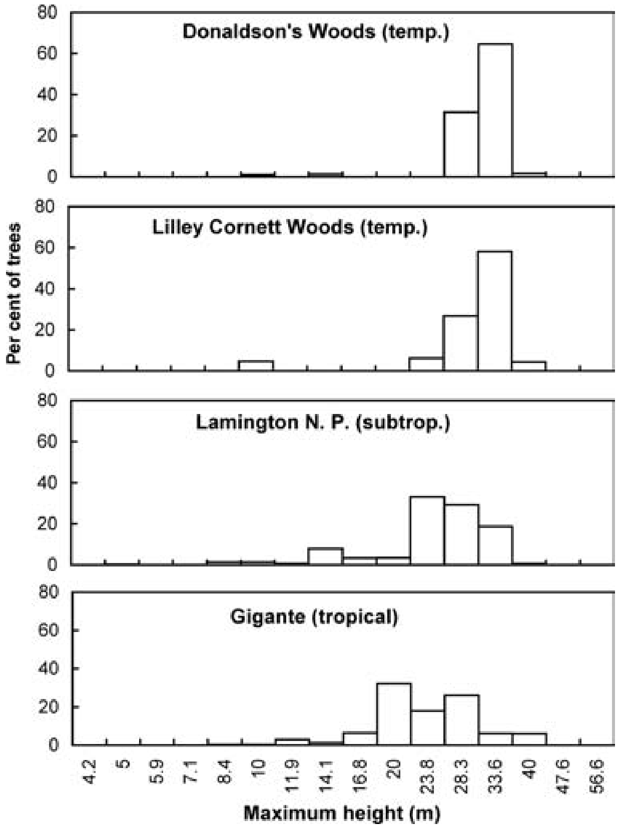

Figure 3. Per cent of trees ≥ 10 cm dbh belonging to species whose maximum height falls within each quarter octave height class. Heights listed along the abscissa are lower limits of quarter octave height classes.

Table 3. The overall densities of trees and the percentages of those trees belonging to canopy species ($h_{max} \geq 28.3$ m) for two diameter classes. Density refers to all species; percentages to those species for which h_{max} was measured (making up >62% of the stems in all cases). Data for Donaldson's Woods, Lilley Cornett Woods, and the subtropical and tropical (Gigante) sites are from Schmeltz *et al.* (1974), Muller (1982) and this study, respectively.

	Trees 2.5–10 cm dbh		Trees 10–20 cm dbh	
Site	Trees ha^{-1}	% stems of canopy spp.	Trees ha^{-1}	% stems of canopy spp.
Donaldson's			112	95
Lilley Cornett*	784	79		
Subtropical	2140	15	301	30
Tropical	1847	17	331	27

*Species abundances at this site were given for 2.5–10 cm dbh and ≥10 dbh trees, but not 10–20 cm dbh trees.

for seedling survival (studentized residual > 6) and was therefore excluded from this analysis only. The interaction between tree stature (understorey vs. canopy species) and seed mass was insignificant for both seed survival ($F_{1,54} = 1.98$, $P = 0.17$) and seedling survival ($F_{1,45} = 1.25$, $P = 0.27$). Survival increased with seed mass for both seeds ($F_{1,55} = 21.2$, $P < 0.001$) and seedlings ($F_{1,46} = 10.3$, $P < 0.01$); and survival was greater for understorey trees than for canopy trees after controlling for the influence of seed mass for both seeds ($F_{1,55} = 30.3$, $P < 0.001$) and seedlings ($F_{1,46} = 6.21$, $P < 0.05$).

DISCUSSION

General patterns

Our results suggest that temperate deciduous forests of North America differ markedly from tropical

Table 4. Diversity of canopy species ($h_{max} \geq 28.3$ m) and all species attaining 10 cm dbh for the enumerated sites. Fisher's α is defined by $S = \alpha \ln(1 + N/\alpha)$, where S and N represent the number of species and individuals enumerated, respectively (Leigh 1999). At Lamington and Gigante, the numbers of canopy species and stems of these species (among all stems $\geq$10 cm dbh) were estimated assuming the same proportions of species and trees of this stature range as measured among the more common species (Table 2).

Site	Sample area (ha)	Number of trees		Number of species		Fisher's α	
		Canopy	All trees	Canopy	All trees	Canopy	All trees
Donaldson's Woods, USA	7.9	2141	2200	20	25	3.1	4.0
Lilley Cornett Woods, USA	1.92	707	788	22	28	4.3	5.7
Lamington, N.P., Australia	1.94	656	1349	30	75	6.5	17.1
Gigante, Panama	5.76	828	2158	45	155	10.2	38.3

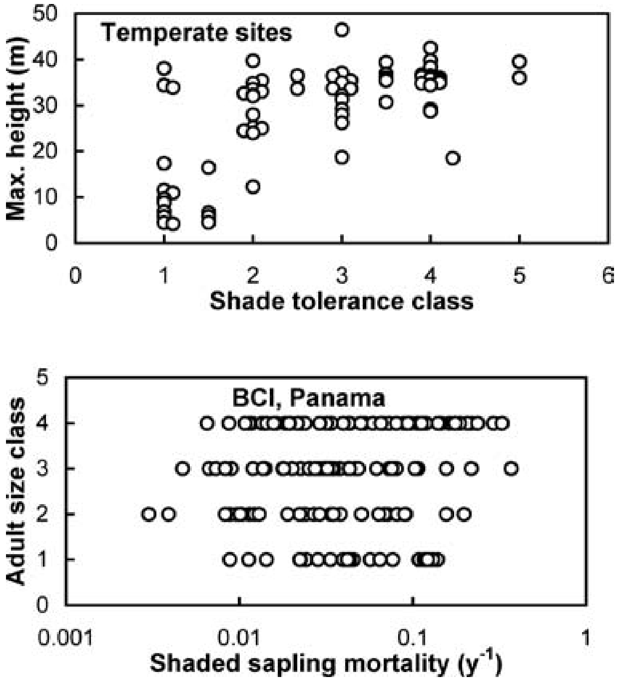

Figure 4. Species stature and shade tolerance for the seven deciduous forest sites and the 50-ha plot on Barro Colorado Island, Panama. Shade tolerance classes 1–5 are, respectively, very tolerant, tolerant, intermediate, intolerant and very intolerant of shade, as rated by foresters (Baker 1949, Burns & Honkala 1990), or in the case of the smallest-statured species, by the authors, based on co-occurrence in shade with saplings of shade-tolerant trees and other studies of these species (e.g. Lei & Lechowicz 1990). Shaded sapling mortalities for BCI are for saplings under canopies >10 m tall (Welden *et al.* 1991); adult size classes 1–4 are, respectively, shrubs, treelets, mid-sized trees and large trees, as defined by Condit *et al.* (1996). Some points were jiggled slightly to the right or left to reduce overlap in the upper panel.

forests in the distribution of adult statures of their constituent species. The deciduous forests showed greater dominance by canopy trees (Figure 3) and much higher proportions of large species than did the tropical forests (Figure 2). Extreme dominance by overstorey species was also found for the tall (60 to 100+ m) old-growth coniferous forests of the North American west coast (Van Pelt & Franklin 2000). A relatively continuous

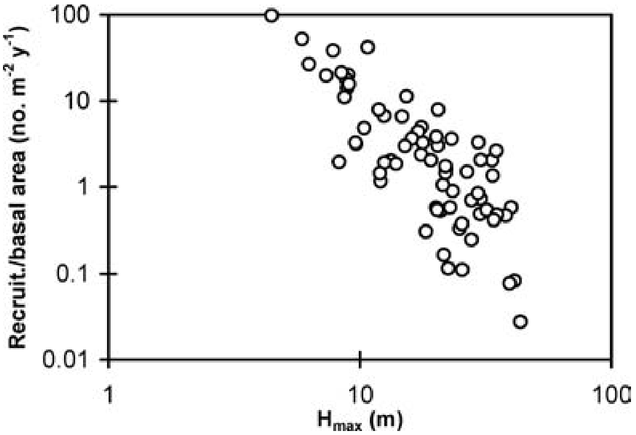

Figure 5. Estimated sapling recruitment per unit stem basal area vs. maximum height per species at Gigante, Panama. The 70 species had at least three 1–1.9-cm-dbh saplings on the sapling subplots.

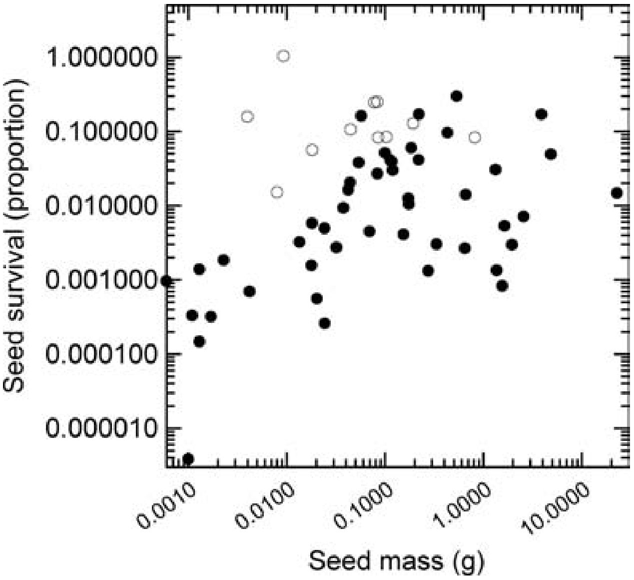

Figure 6. Seed survival is greater for understorey tree species (open symbols) than for canopy tree species (closed symbols) on Barro Colorado Island, Panama. Understorey trees include shrubs and treelets and canopy trees include mid-sized and large trees, as defined by Condit *et al.* (1996).

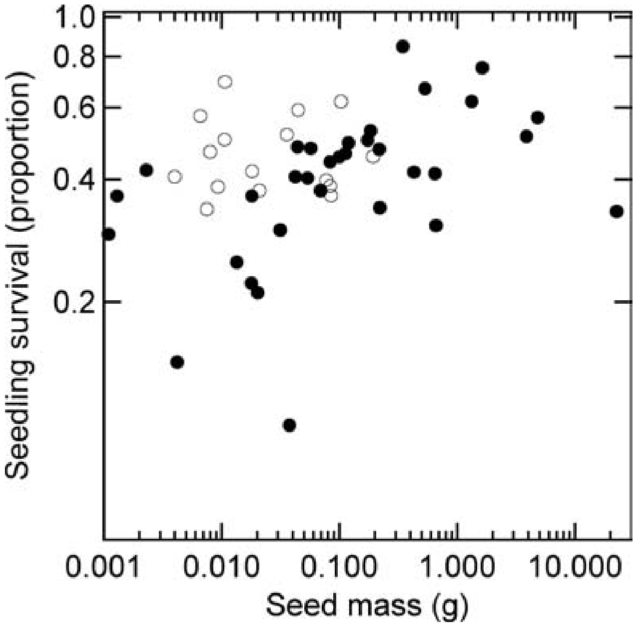

Figure 7. First-year seedling survival is greater for understorey tree species (open symbols) than for canopy tree species (closed symbols) on Barro Colorado Island, Panama. Understorey trees include shrubs and treelets and canopy trees include mid-sized and large trees, as defined by Condit *et al.* (1996).

distribution of maximum tree heights was observed for both a warm-temperate evergreen angiosperm forest and a montane temperate deciduous forest in southern Japan (Aiba & Kohyama 1996, Koike & Hotta 1996). The Japanese forests were, however, considerably shorter (22- and 29-m maximum height, respectively) than the tall (~40 m) North American forests studied here, and most species in the montane forest were less than half the height of the tallest species.

The marked difference in the proportions of large vs. smaller species among the study forests was associated with corresponding differences in tree diversity. For the Panamanian and subtropical sites, a sample containing a given number of stems will include many more species if drawn from all trees than if it is restricted to large species, as indicated by contrasting values of Fisher's α (Table 4). This pattern is consistent with the observation of higher α values for small-statured species than for canopy species in a wet tropical forest in Sri Lanka (Gunatilleke *et al.* 2004). Thus, diversification in tree stature contributes greatly to tropical tree diversity, but is less important in tall temperate forests of North America.

Within diverse tropical forests there is substantial diversification in maximum height among co-occuring species of the more speciose genera (Davies *et al.* 1998, Thomas 1996). At Gigante, Panama, nine of the 14 genera with two or more measured species showed a within-genus range in h_{max} of more than 1.5 fold (Appendix 3). In contrast, only three of the 12 temperate genera with two or more measured species showed a range this large (Appendix 1). These three are *Cornus*, *Magnolia* and especially, *Acer*, which shows similar patterns in Eurasia (Ackerly & Donoghue 1998). Small-statured species do occur among some of the other large-statured genera of this study (e.g. *Quercus*), but they are usually restricted to short forests on unfavourable sites.

Tree size distributions and the proportions of smaller stems that are juveniles of large-statured species also appear to differ with latitude. As observed by Hartshorn (1978), tropical forests have higher densities of small individuals (2.5–20 cm dbh) than do old-growth temperate deciduous forests. This greater density was associated with the dominance of smaller-statured species among stems of 2.5–20 cm dbh at both the tropical and subtropical sites (Table 3).

Coexistence of species of differing stature

Kohyama (1993, 1996) used a forest dynamics model to demonstrate that the number of species that can coexist increases with the range in adult height of the constituent species. However, coexistence was only predicted for limited ranges in the establishment, growth and mortality rates of the constituent species and these allowable ranges decreased with increasing species packing along the height gradient.

A necessary condition for the coexistence of species with identical mortality and growth functions (relating growth to current size, maximum size and stand basal area) is that sapling recruitment per unit basal area must increase as maximum size decreases (Kohyama 1993, 1996). This condition was met by the species of the warm temperate rain forest to which the model was applied, a South-East Asian forest (Kohyama *et al.* 2003) and the Panamanian site considered here (Figure 5). On Barro Colorado Island, near this site, understorey species showed greater seedling establishment per seed and greater seedling survival rates than did larger-statured species (Figures 6 and 7). At Pasoh Forest, Malaysia, saplings of understorey species tend to have lower photosynthetic light compensation points and lower photosynthetic capacities than do saplings of larger-statured species (Thomas & Bazzaz 1999). Thus, adaptations for rapid growth under high light in canopy species may result in lower seedling shade tolerance than in understorey species, despite considerable plasticity and interspecific differences within both groups (Thomas 2003, Thomas & Bazzaz 1999, Turner 2001, Valladares *et al.* 2000, Welden *et al.* 1991). As only about 1 of 100,000 seeds produced on Barro Colorado grow into saplings ≥ 1 cm dbh (Harms *et al.* 2000), small differences in mortality rates may have substantial effects on sapling recruitment and hence species coexistence.

Density-dependent death of seedlings may be associated with the build-up of host-specific pests and pathogens on conspecific leaf litter and seedlings on the forest floor (Leigh 1999). Because small understorey trees produce far less leaf litter and seed mass per tree than do canopy trees, they are effectively rarer with respect to such effects. This inference is supported by the observation of decreasing density-dependent effects on sapling recruitment with decreasing adult size on Barro Colorado Island, with the exception of the most common treelet species, *Faramea occidentalis* (Condit *et al.* 1992, Leigh 1999). Thus, density-dependent processes thought to favour rare species may also contribute to the observed higher recruitment efficiency of understorey species.

Possible causes of latitudinal shifts in tree stature distributions

The current distribution of adult tree statures within forests is influenced by the regional species pool and the relative abilities of species of differing size to compete or coexist. Factors that may influence relative abilities to compete and that differ between tropical and temperate regions include growing season length, sun angle and tree crown shape.

A year-round growing season and leaf life spans of 1 – 4 + y among understorey plants (Coley 1988) make it possible to recover leaf construction costs over longer periods and may therefore lower whole-plant light compensation points in the tropics (Givnish 1988, Terborgh 1985). Somewhat less light penetrates to the forest floor in tropical vs. temperate deciduous forests (Brown & Parker 1994, Leigh 1999, Richards 1996), consistent with lower whole-plant light compensation points and hence greater utilization of light by tropical understorey trees. As a result, wet tropical forests support greater leaf area per unit ground area (LAI) than do temperate deciduous forests (Leigh 1999) and vertical transects in tropical forests commonly encounter crowns of several trees or saplings, one beneath the other (Koike & Syahbuddin 1993).

High midday sun angles enhance penetration of incident light into canopy gaps and to the vegetation below in equatorial forests (Canham *et al.* 1990). However, gaps providing direct illumination of the ground are ephemeral in tropical forests, due to the germination of fast-growing pioneer species and the vigorous growth response of existing vegetation (Denslow 1987). Gaps between canopy trees are ubiquitous, and gaps that reach down to the forest floor are usually wider at higher levels within forests (Connell *et al.* 1997, Hubbell & Foster 1986). This extra light associated with upper-level gaps is essential for the maturation of most canopy species (Canham 1985) and increases the reproductive output of understorey trees (Levey 1988). Thus, the beneficial influence of upper canopy gaps on adult understorey and midstorey trees may have larger effects on diversity than the small, shifting area of ephemeral gaps reaching down to the forest floor. Furthermore, the abundance of these smaller-statured species, along with lianas (Putz 1984), may also aid in maintaining upper level openings by retarding their closure by large-statured species. In contrast, the tendency for crown depth in canopy trees to increase with increasing latitude (Kuuluvainen 1992), coupled with changes in sun angle, reduces the penetration of light into gaps in high-latitude forests (Canham *et al.* 1990), thereby increasing the competitive advantage of overstorey vs. understorey trees with increasing latitude. This reduced light penetration may also explain the lack of small-statured shade-intolerant species at the temperate sites (Figure 4); these species are typically associated with persistent openings, such as stream banks, or widespread disturbances, such as stand-replacing fires (Fernald 1950). Thus, the combined effects of sun angle, overstorey crown geometry and a year-round growing season may act synergistically to provide a relative advantage to understorey and midstorey trees at low latitudes by increasing light penetration to the crowns of these trees and by increasing their capacity to subsist on limited light (Terborgh 1985).

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Appendix 1. Maximum heights (m) of species of temperate deciduous forests of the USA. Locations are: 1. Mohawk Trail State Forest, Massachussetts, 2. Brown County, Indiana, 3. Donaldson's Woods, Indiana, 4. Beall Woods, Illinois (floodplain section), 5. Lilley Cornett Woods, Kentucky, 6. Big Oak Woods, North Carolina and 7. selected cove forests of Great Smoky Mountains National Park, Tennessee. Maximum heights are means of the one to three tallest trees encountered in limited search times (see Methods).

		h_{max} (m) for site no.						
Species	Family	1	2	3	4	5	6	7
Acer negundo L.	Aceraceae				24.5			
Acer pensylvanicum L.	Aceraceae	16.85						17.9
Acer rubrum L.	Aceraceae	34.2		34		35	27.5	37.2
Acer sacharinum L.	Aceraceae				34.8			
Acer saccharum Marsh.	Aceraceae	35.6	31.8	32		34		36
Acer spicatum Lam.	Aceraceae	8.5						9.1
Aesculus flava Ait.	Hippocastanaceae							39.7
Asimina triloba (L.) Dunal	Annonaceae		11.7	11.8	11	11.2		
Betula alleghaniensis Britton	Betulaceae	29.4						29
Betula lenta L.	Betulaceae	31.2				28.2		32.6
Betula papyrifera Marsh.	Betulaceae	28.7						
Carpinus caroliniana Walt.	Betulaceae		9.1	9.2			10.7	
Carya cordiformis (Wangenh.) K. Koch	Juglandaceae		35.5	31	33	35.5		39
Carya glabra (Mill.) Sweet	Juglandaceae					36		
Carya illinoensis (Wangenh.) K. Koch	Juglandaceae				36.2			
Carya lacinosa (Michx. f.) Loud.	Juglandaceae				33.6			
Carya ovata (Mill.) K. Koch	Juglandaceae		33	35.2		38		
C. ovata and/or *Carya carolinae-septentrionalis* (Ashe) Engl. & Graeb.	Juglandaceae						35.7	
Carya tomentosa (Poir.) Nutt.	Juglandaceae					39.8		
Celtis laevigata Willd.	Ulmaceae				28			
Celtis occidentalis L.	Ulmaceae				31.3			
Cercis canadensis L.	Fabaceae			13.3		11.2		
Cladrastis kentukea (Dum.-Cours.) Rudd	Fabaceae		25.2					
Cornus alternifolia L.	Cornaceae	6.8						
Cornus florida L.	Cornaceae		11.5	11.4		11.4	9.4	
Fagus grandifolia Ehrh.	Fagaceae	35.6	33.7	35.5		33		34.3
Fraxinus americana L.	Oleaceae	40.6	37	36.2	33.5	36.5		37.4
Fraxinus pennsylvanica Marsh.	Oleaceae				36.5			
Gymnocladus dioicus (L.) K. Koch	Fabaceae				34.4			
Halesia carolina L.	Styracaceae							32.6
Hamamelis virginiana L.	Hamamelidaceae	5.7	4.8					6.9
Ilex decidua Walt.	Aquifoliaceae						6.6	
Juniperus virginiana[b] L.	Cupressaceae						18.5	
Juglans nigra L.	Juglandaceae		35	34	34.2	36.5		
Lindera benzoin (L.) Blume	Lauraceae		4.4		4.4	4.6		
Liquidambar styraciflua L.	Hamamelidaceae				38.5		34.5	
Liriodendron tulipifera L.	Magnoliaceae		40	40		45.1		44.8
Magnolia acuminata L.	Magnoliaceae					33.5		36.4
Magnolia fraseri Walt.	Magnoliaceae							33.6
Magnolia macrophylla Michx.	Magnoliaceae					26.2		
Magnolia tripetala L.	Magnoliaceae					18.7		
Nyssa sylvatica Marsh.	Nyssaceae		30	34				
Ostrya virginiana (Mill.) K. Koch	Betulaceae	19	16	14.4				
Oxydendrum arboreum (L.) DC.	Ericaceae					24		
Pinus strobus[b] L.	Pinaceae	46.5						
Pinus taeda[b] L.	Pinaceae						36	
Platanus occidentalis L.	Platanaceae				39.4			
Populus deltoides Bartr. ex Marsh.	Salicaceae				39.5			
Prunus serotina Ehrh.	Rosaceae	34.2	37					38
Quercus alba L.	Fagaceae		34.5	35.4		39	32.8	
Quercus falcata var. *pagodifolia* Ell.	Fagaceae						35.8	
Quercus macrocarpa Michx.	Fagaceae				37.1			
Quercus michauxii Nutt.	Fagaceae						35.5	
Quercus phellos L.	Fagaceae						36.7	
Quercus prinus L.	Fagaceae		33.7					
Quercus rubra L.	Fagaceae	37.5	34.8	34.7		38		38
Quercus shumardii Buckl.	Fagaceae				38.3			

Appendix 1. Continued.

Species	Family	h_{max} (m) for site no.						
		1	2	3	4	5	6	7
Quercus velutina Lam.	Fagaceae		30	33		33.5		
Rhododendron maximum[a] L.	Ericaceae					5.1		6.5
Robinia pseudoacacia L.	Fabaceae							36
Sassafras albidum (Nutt.) Nees	Lauraceae		29.2					
Tilia americana L.	Tiliaceae	34	32					
Tilia heterophylla Vent.	Tiliaceae					35.6		35.2
Tsuga canadensis[b] (L.) Carr.	Pinaceae	34				38		42.2
Ulmus alata Michx.	Ulmaceae						25	
Ulmus americana L.	Ulmaceae				28			
Ulmus rubra Muhl.	Ulmaceae		31.8	32.8				
Viburnum alnifolium L.	Caprifoliaceae							4.2
Viburnum prunifolium L.	Caprifoliaceae						4.5	

[a] Evergreen angiosperm.

[b] Evergreen conifer.

Appendix 2. Maximum heights of species in the plot of Connell *et al.* (1984) in Lamington, National Park, Queensland, Australia.

Species	Family	h_{max} (m)
Actephila lindleyi (Steudel) Airy Shaw	Euphorbiaceae	9
Acronychia pubescens (F. Muell.) C. T. White	Rutaceae	18
Acronychia suberosa C. T. White	Rutaceae	21.6
Argyrodendron actinophyllum (F. M. Bailey) Edlin	Sterculiaceae	33.2
Argyrodendron trifoliolatum F. Muell.	Sterculiaceae	37
Baloghia inophylla (Forst. F.) P. S. Green	Euphorbiaceae	24
Baurella simplicifolia (Endl.) T. Hartley	Rutaceae	23.5
Caldcluvia paniculosa (F. Muell.) Hoogland	Cunoniaceae	28.2
Clerodendrum floribundum R. Br.	Verbenaceae	13
Cinnamomum virens R. T. Baker	Lauraceae	31.5
Denhamia pittosporoides F. Muell.	Celastraceae	16
Diospyros pentamera Woods & F. Muell. ex F. Muell.	Ebenaceae	27.8
Diploglottis cunninghamii Hook. F.	Sapindaceae	28.5
Doryphora sassafras Endl.	Monimiaceae	31
Ellatostachys nervosa (F. Muell.) Radlk.	Sapindaceae	23
Emmenosperma alphitonioides F. Muell.	Rhamnaceae	34.1
Euodia micrococca F. Muell.	Rutaceae	24.8
Eupomatia laurina R. Br.	Eupomatiaceae	10.5
Ficus watkinsiana F. M. Bailey	Moraceae	40
Geissois benthamii F. Muell.	Cunoniaceae	29
Halfordia kendack (Montr.) Guillaumin	Rutaceae	26.5
Litsea reticulata (Meisn.) F. Muell.	Lauraceae	31
Melicope octandra (F. Muell.) Druce	Rutaceae	30.8
Mischocarpus pyriformis (F. Muell.) Radlk.	Sapindaceae	19
Orites excelsa R. Br.	Proteaceae	28.8
Polyscias elegans (C. Moore & F. Muell.) Harms	Araliaceae	25.7
Premna lignum-vitae (Cunn. ex Schauer) Pieper	Verbenaceae	32.5
Pseudoweinmannia lachnocarpa (F. Muell.) Endl.	Cunoniaceae	35.2
Psychotria simmondsiana F. M. Bailey	Rubiaceae	4.9
Quintinia sieberi A. DC.	Escalloniaceae	16.2
Randia benthamiana F. Muell.	Rubiaceae	14.8
Sarcopteryx stipitata (F. Muell.) Radlk.	Sapindaceae	25
Synoum glandulosum (Sm.) A. Juss.	Meliaceae	17.5
Syzygium crebrenerve (C. T. White) L. Johnson	Myrtaceae	31
Tasmannia insipida R. Br. ex DC.	Winteraceae	6.2
Wilkiea austroqueenslandica Domi.	Monimiaceae	9.4
Wilkiea huegeliana (Tul.) A. DC.	Monimiaceae	5.4

Appendix 3. Maximum heights of species in the 38.4 ha plot on the Gigante peninsula of the Barro Colorado Nature Monument, Panama. Nomenclature of D'Arcy (1987), as updated by Condit *et al.* (1996).

Species	Family	h_{max} (m)
Alseis blackiana	Rubiaceae	30.2
Amaioua corymbosa	Rubiaceae	17.8
Apeiba aspera	Tiliaceae	32.7
Ardisia fendleri	Myrsinaceae	13.0
Aspidospermum cruentum	Apocynaceae	39.9
Beilschmiedia pendula	Lauraceae	30.1
Brosimum alicastrum	Moraceae	35.0
Brosimum guianensis	Moraceae	29.6
Calophyllum longifolium	Clusiaceae	34.8
Cassipourea elliptica	Rhizophoraceae	22.8
Copaifera aromatica	Fabaceae	35.0
Cordia bicolor	Boraginaceae	25.5
Cordia lasiocalyx	Boraginaceae	12.0
Coussarea curvigemmia	Rubiaceae	7.3
Couratari guianensis	Lecythidaceae	31.5
Desmopsis panamensis	Annonaceae	9.0
Dialium guianense	Fabaceae	30.2
Diospyros artanthifolia	Ebenaceae	20.3
Dipteryx panamensis	Fabacaceae	43.4
Drypetes standleyi	Euphorbiaceae	22.4
Eugenia coloradoensis	Myrtaceae	21.9
Faramea luteovirens	Rubiaceae	5.9
Faramea occidentalis	Rubiaceae	16.1
Garcinia intermedia	Clusiaceae	20.5
Garcinia madruno	Clusiaceae	20.1
Guatteria dumetorum	Annonaceae	33.3
Heisteria acuminata	Olacaceae	12.5
Heisteria concinna	Olacaceae	20.4
Hirtella americana	Chrysobalanaceae	20.9
Hirtella racemosa	Chrysobalanaceae	7.8
Hirtella triandra	Chrysobalanaceae	23.4
Hybanthus prunifolius	Violaceae	6.3
Inga cocleensis	Fabaceae	21.9
Inga umbellifera	Fabaceae	12.5
Jacaranda copaia	Bignoniaceae	31.9
Lacistema aggregatum	Flacourtiaceae	9.0
Lacmellea panamensis	Apocynaceae	23.4
Laetia procera	Flacourtiaceae	27.3
Laetia thamnia	Flacourtiaceae	14.7
Licania hypoleuca	Chrysobalanaceae	22.0
Lonchocarpus latifolius	Fabaceae	32.0
Mabea occidentalis	Euphorbiaceae	13.3
Mosannona garwoodii	Annonaceae	15.1
Miconia argentea	Melastomaceae	19.1
Miconia minutiflora	Melastomaceae	25.8
Mouriri myrtilloides	Melastomaceae	8.8
Myrcia sp.	Myrtaceae	9.6
Myrcia gatunensis	Myrtaceae	13.9
Myrcia zetekeniana	Myrtaceae	4.5
Nectandra purpurea	Lauraceae	21.4
Ouratea lucens	Ochnaceae	8.4
Oxandra panamensis	Annonaceae	17.6
Perebea xanthochyma	Moraceae	17.0
Phoebe cinnamomifolia	Lauraceae	24.7
Pachira sessilis	Bombacaceae	38.1
Poulsenia armata	Moraceae	26.6
Pourouma bicolor	Cecropiaceae	25.5
Pouteria reticulata	Sapotaceae	29.5
Prioria copaifera	Fabaceae	41.5
Protium sp.	Burseraceae	17.5
Protium panamense	Burseraceae	23.1
Protium correae	Burseraceae	15.3
Protium tenuifolium	Burseraceae	25.5
Quassia amara	Simaroubaceae	11.9
Rinorea crenata	Violaceae	8.2
Rinorea squamata	Violaceae	12.1
Rinorea sylvatica	Violaceae	10.7
Simarouba amara	Simaroubaceae	27.8
Sloanea zulianensis	Elaeocarpaceae	18.3
Sorocea affinis	Moraceae	8.9
Sterculia recordiana	Sterculiaceae	26.6
Swartzia panamensis	Fabaceae	21.5
Swartzia simplex var. *ochnacea*	Fabacaceae	8.7
Tabebuia guayacan	Bignoniaceae	39.4
Tachigali versicolor	Fabaceae	33.7
Talisia nervosa	Sapindaceae	9.6
Tetragastris panamensis	Burseraceae	33.5
Tovomita stylosa	Clusiaceae	10.4
Trattinnickia aspera	Burseraceae	30.1
Trichilia tuberculata	Meliaceae	24.9
Vatairea lundellii	Fabacaceae	41.2
Virola sebifera	Myristicaceae	27.8
Virola multiflora	Myristicaceae	34.1
Virola surinamensis	Myristicaceae	37.0
Xylopia macrantha	Annonaceae	20.1