

Maximum size distributions in tropical forest communities: relationships with rainfall and disturbance

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Summary

1. The diversity and structure of communities are partly determined by how species partition resource gradients. Plant size is an important indicator of species position along the vertical light gradient in the vegetation.
2. Here, we compared the size distribution of tree species in 44 Ghanaian tropical forest communities, using data from 880 one-hectare plots and over 118 000 trees belonging to more than 210 species.
3. The size distribution of forest species showed a continuous normal or log-normal distribution, with many canopy species and a few large species, and varied from community to community. Multiple regression showed that this variation is related to rainfall and to disturbance.
4. Size distributions in wet forests were less skewed than those in dry forests, with a smaller proportion of big species and a smaller size range. At the same time they exhibited tighter species packing, resulting in higher species richness. Communities with high disturbance have less species packing and lower species richness.
5. *Synthesis.* We conclude that the factors that constrain organism size and species coexistence in these tropical forest tree communities differ from those known to operate on a number of well-studied animal communities.

Key-words: adult stature, coexistence, disturbance, Ghana, light, potential height, rainfall, species packing, species richness, tropical forest

Introduction

The diversity and structure of plant and animal communities are partly determined by how species partition resource gradients. More species can be packed into a habitat when resource gradients are longer, and when species have either narrower or more overlapping niches (Begon *et al.* 1990). Many animal studies have focused on body size as an indicator of how species partition resources (Hutchinson & MacArthur 1959; Prins & Olf 1998; Ritchie & Olf 1999). In plant studies there has been a recent renewal of interest in size as an important indicator of plant strategy and species position along resource gradients (Kohyama 1992; Westoby 1998; Turner 2001; McGill *et al.* 2006). Within plant communities there is a strong vertical gradient in light, from full irradiance above the canopy, to less than a few percent irradiance at the bottom of the stand. Species that are a little taller than their neighbours potentially intercept more light (Hirose & Werger 1994), and

competition for light is therefore highly asymmetric (Schwinning & Weiner 1998). This size advantage suggests an evolutionary race between species for ever-increasing height. Tropical rain forests, in which the canopy can attain a height of up to 50 m, can arguably be seen as an extreme case of such competition, because of its very tall canopy. Yet, within rain forest communities species differ tremendously in their potential height, from 1 m up to 70 m (Richards 1952). Tall and small species may coexist because they are adapted to different parts of the light gradient (Thomas & Bazzaz 1999), and because of a trade-off between maximum size and time till maturity (Kohyama 1992). In general, the size distribution may differ between taxonomic groups and communities. Sometimes a unimodal distribution of species sizes is found (Ritchie & Olf 1999), whereas others predict, on theoretical grounds, a multimodal distribution (Scheffer & van Nes 2006).

The distribution of maximum species sizes and the packing of species in communities may vary along environmental gradients. Despite the potential importance of differences in height, there have been few quantitative studies of size

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distribution of tree species in different forest communities. King *et al.* (2006) evaluated size distribution in nine forests along a latitudinal gradient. Temperate forests were characterized by a large proportion of canopy species, a virtual absence of subcanopy tree species, and few understorey tree species. In contrast, wet tropical forests showed a more continuous distribution in species' heights, in which the greater number of subcanopy and understorey species explained most of their higher species diversity (cf. Niklas *et al.* 2003a). King *et al.* (2006) have suggested that tropical forests contain relatively more subcanopy and understorey species than temperate forests because the longer growing season allows for longer leaf life spans, lower whole-plant light compensation points and a higher degree of shade tolerance.

Here, we compare the size distributions of tree species in 44 tropical forest communities. We selected our data from a large systematic forest inventory in Ghana of 880 one-hectare plots and over 118 000 trees. We use the observed maximum d.b.h. as an indicator of the maximum size of the species because observed maximum diameter can be measured precisely from sample data, and because diameter scales closely with the height, crown exposure, crown area and biomass of individual trees (Muller-Landau *et al.* 2006), and maximum diameter scales closely with maximum height (King *et al.* 2006), maximum crown area and average crown exposure of tree species (L. Poorter, unpublished data). In this paper, we use the terms maximum diameter and maximum size somewhat interchangeably, though the first term emphasizes our empirical analyses and the second the more general concepts which we shall briefly elaborate.

Maximum size is considered a proxy of species position along the vertical light gradient in the forest canopy, as tall species experience higher light levels over their lifetime than small species (Poorter *et al.* 2005). Maximum size also reflects how much light each species can potentially intercept and pre-empt, as bigger species have wider crowns. For example, across 52 Bolivian moist forest tree species, the maximum crown area scales closely with the maximum diameter of the species (crown area = $0.34 D_{\max}^{1.36}$, $r^2 = 0.85$, $P < 0.001$; L. Poorter, unpublished data). Species packing was defined as the number of tree species divided by the whole species diameter size range found in the forest. We evaluate how size structure and species packing vary along gradients of rainfall and disturbance, as these gradients are known to have important effects on community composition and structure in the tropics (Huston 1994; Poorter *et al.* 2004; ter Steege *et al.* 2006). Rainfall is closely linked to plant water availability and ecosystem productivity (Lieth 1975).

Disturbances such as storms, fires and logging open up the forest canopy, leading to increased light penetration and greater regeneration of pioneer species (Hawthorne 1994; Sheil & Burslem 2003; ter Steege 2003). In this study, we used the proportion of trees belonging to pioneer species in each forest as a simple indicator of disturbance history.

We sought predictions to guide our analysis. Little is known about the packing of tree species in relation to species size. Nonetheless, various concepts do appear potentially

relevant. Based on simple (and debatable) assumptions we made the following testable predictions:

1 Species will follow a unimodal size distribution as found in many animal studies. Alternatively, recent theoretical research (Scheffer & van Nes 2006) suggests that species-rich communities may be structured with a series of distinctive life-history strategies partitioning the resource gradient. If this is true for the vertical light gradient in forests, a multimodal distribution of species sizes is predicted.

2 The size range of tree species in a community increases with an increase in rainfall and decreases with higher disturbance. Higher rainfall typically implies higher productivity, leading to taller and thicker trees and hence a larger range of species sizes. High disturbance leads to high mortality rates, thus preventing many trees from attaining their maximum sizes, and it also reduces the ability of slower-growing species to reach reproductive sizes (Sheil *et al.* 2006). Both effects result in a smaller range of actual species sizes (cf. Niklas *et al.* 2003b).

3 The proportion of small species may either increase or decrease with rainfall, but will increase with an increase in disturbance. Following the line of reasoning of King *et al.* (2006), wetter forests have longer growing seasons, which allows for longer leaf life spans, increased shade tolerance and hence more small understorey stems and species. Alternatively, drier forests have a semi-deciduous forest canopy in the dry season, which leads to a light pulse in the forest understorey, allowing more small understorey stems and species to realize a positive carbon balance and coexist (Quigley & Platt 2003). A high disturbance regime leads to open sites that can be colonized by new species. These might be short-lived pioneer species that are inherently small (Falster & Westoby 2005), or longer-lived species that are inherently taller, but have colonized the area too recently to have attained their maximum size. A preponderance of small diameter species may also reflect the disadvantage of larger species when subjected to repeated disturbance events (Sheil *et al.* 2006).

4 The number of species that partition a certain size range (i.e. species packing) will increase with rainfall and decrease with disturbance. The absence of seasonal drought stress in high rainfall areas may lead to a higher degree of specialization, and hence, more species packing. A high disturbance regime prevents the community from being fully saturated with species, leading to lower species richness and reduced species packing.

Methods

A country-wide forest inventory was carried out by the Forestry Department of Ghana in collaboration with the UK's Overseas Development Administration (now 'DfID') (for background see Hawthorne & Abu-Juam 1995; Hawthorne 1996). One hundred twenty-seven forest reserves were systematically sampled on a 2×2 -km grid. At each intersection of this grid a 1-ha plot was established, in which trees were inventoried in a nested design. All living trees ≥ 30 cm d.b.h. were sampled over the whole area, trees 10–30 cm d.b.h. in 0.1 ha subplots, and trees 5–10 cm d.b.h. in 0.05 ha subplots. All trees were identified and had their d.b.h. measured.

For our study, we selected all 44 reserves that had at least 20 one-hectare plots. For each reserve we randomly selected 20 plots from all measured plots in the reserve, to ensure a similar sampling size between reserves. In this way, for each reserve, small diameter trees were recorded in 1 ha, intermediate trees in 2 ha and large trees in 20 ha. In total, 880 one-hectare plots and 118 403 trees were analyzed. The 44 reserves cover most of the forest gradient in Ghana (cf. Hall & Swaine 1976) from wet evergreen forest in the southwest to dry deciduous forest in the northeast (the two driest forest types are not represented as forest reserves in these zones are too small). For each reserve the latitude and longitude of the reserve centre was determined. Environmental conditions were estimated using the central location of the reserves and maps of annual rainfall (mm year^{-1}), soil fertility (CMK, in cmol cations kg^{-1} soil) and altitude (Bongers *et al.* 2004). Based on these assessments the estimated rainfall of the 44 reserves varied from 1205 to 2147 mm year^{-1} , the soil fertility from 0.3 to 39.3 cmol cations (Ca^{2+} , Mg^{2+} , K^{+}) kg^{-1} , and the altitude from 72 to 448 m.

For each reserve the percentage of trees belonging to pioneer species was calculated, based on all plots in the reserve. Hawthorne (1995) classified the Ghanaian tree species into four regeneration guilds; pioneers that need gaps for establishment, non-pioneer light demanders that can establish in shade but need a gap to grow to larger sizes, shade bearers that can be found as young and old plants in shade and cryptic pioneers which establish in gaps but typically develop in the understorey and a fifth guild, the swamp species. We calculated %pioneers as the percentage of inventoried trees with known guilds that belonged to the pioneer group. On average 4% of stems in each reserve belonged to species that could not be classified. We calculated the %pioneers for two size classes (5–30 and over 30 cm d.b.h.) to be able to distinguish between recent disturbance (reflected in the small size classes), and old disturbance (reflected in the large size classes). Both indices were strongly correlated ($r = 0.81$, $P < 0.001$, $n = 44$) suggesting that the general pattern of relative intensity of disturbance has not changed much over time. We therefore devised and used one pioneer index for the whole stem-size range. To correct for differences in sampling intensity, the small trees (5–10 cm d.b.h.) that were sampled in 1/20th of the area received a weight of 20 in this pioneer index analysis, the intermediate trees (10–30 cm d.b.h.) that were sampled in 1/10th of the area received a weight of 10, and the large trees (≥ 30 cm d.b.h.) that were inventoried in the whole area received a weight of 1. Hawthorne & Abu-Juam (1995) evaluated the condition of the Ghanaian forest reserves on an ordinal scale from 1 (no or few signs of disturbance) to 5 (seriously degraded with more than three quarters of the canopy disturbed or more than half of the forest with scarred stems or burned). Our %pioneer index was significantly correlated with forest condition (Spearman's $r = 0.67$, $P < 0.001$, $n = 44$), suggesting that it is a reasonable indicator of disturbance.

D_{MAX} CALCULATION

For each of the 44 reserves, the maximum d.b.h. (D_{max}) was determined for each species with at least 10 recorded individuals. This minimum number of individuals was used to get a reliable estimate of the maximum size that species can attain in a community; in our data set, the D_{max} of a species in a reserve increased curvilinearly against the number of sampled trees, and typically started to level off between 10 and 20 trees. By restricting our analysis to species represented by 10 or more trees, we dealt with an average of 65 species per reserve (range 39–87). This analysis thus represented the most common species (mean 41% of the species present in the 20

plots selected in each reserve, range 30–48%) and most of the trees in that sample (mean 87% of the individuals present in the 20 plots selected in each reserve, range 78–91%).

We recognized some potential pitfalls of working with maximum diameter measures to characterize species populations. D_{max} will be underestimated if not enough individuals are sampled at a site to be able to encounter the largest one. Furthermore D_{max} might sometimes be overestimated, due to field errors, problems with buttresses, or recording errors. To address this, outlying D_{max} values were removed if trees had a D_{max} larger than the average + 2.7 SD, (based on D_{max} values of the same species in 44 reserves). This corresponds to the upper limit of the 99% confidence interval, and was necessary to apply in only 23 out of 2896 species–reserve combinations, that is, < 1%. In these cases the second largest d.b.h. was used. Forest reserves differ in properties such as size class distribution and stem densities that influence the probability of including large individual stems in the sample. If such community properties are correlated with the environmental factors of interest (i.e. rainfall and %pioneers), this may confound the results – or at least complicate their interpretation. The size class distribution affects the probability that a sample of 10 individuals either consists of juveniles only, or includes adults. With fewer adults sampled it becomes more difficult to determine the species' D_{max} in the forest reserve. For each species with 10 or more stems we therefore calculated the proportion of individuals that were juvenile trees (with d.b.h. < 30 cm), and averaged this per reserve. The average proportion of juvenile trees per species per reserve was neither significantly correlated with rainfall ($r = -0.03$, $P = 0.87$) nor with %pioneers ($r = -0.04$, $P = 0.79$), and therefore did not confound the results. Also, when few trees are sampled per species it is more difficult to determine the species' D_{max} in the forest reserve. We therefore calculated the average number of stems per species per reserve. This was neither significantly correlated with rainfall ($r = 0.01$, $P = 0.97$) nor with %pioneers ($r = 0.08$, $P = 0.59$).

We also calculated the 50th (D_{50}) and 95th (D_{95}) percentile d.b.h. for each species in each reserve. To correct for differences in sampling intensity in determining the D_{50} and D_{95} , trees ≥ 30 cm received a weight of 1, while small trees (5–10 cm d.b.h.) received a weight of 20, and the intermediate trees (10–30 cm d.b.h.) a weight of 10. For each of the 44 reserves we calculated the correlation between D_{max} , D_{95} and D_{50} of the species. D_{max} was strongly correlated with D_{95} (average r across 44 reserves is 0.83) and moderately correlated with D_{50} (average $r = 0.42$).

SIZE STRUCTURE OF THE COMMUNITY

For each reserve, we described the size structure of the species in the community (henceforth referred to as 'size distribution'). We used D_{max} to determine the smallest (S_0), median (S_{50}) and largest (S_{100}) stature species in the community, the size range ($S_{\text{range}} = S_{100} - S_0$), the species packing (number of species/size range) and the skewness or asymmetry of the size distribution. Positive skewness indicates a larger tail of large (rather than small) species, and negative skewness indicates a larger tail of small (rather than large) species. In our evaluation of species packing we used only species represented by 10 or more individuals. The number of species included by this criterion is positively correlated with the total number of species found in the complete 20 ha sample included for each reserve ($r = 0.79$, $P < 0.001$, $n = 44$). For each reserve we made a histogram of the size distribution of the species, using 10 diameter size classes. The number of classes is crucial in this respect, as too many classes would lead to apparent gaps in the size distribution and too few classes would lead to a low resolution (Bongers *et al.* 1988). It is recommended that the number

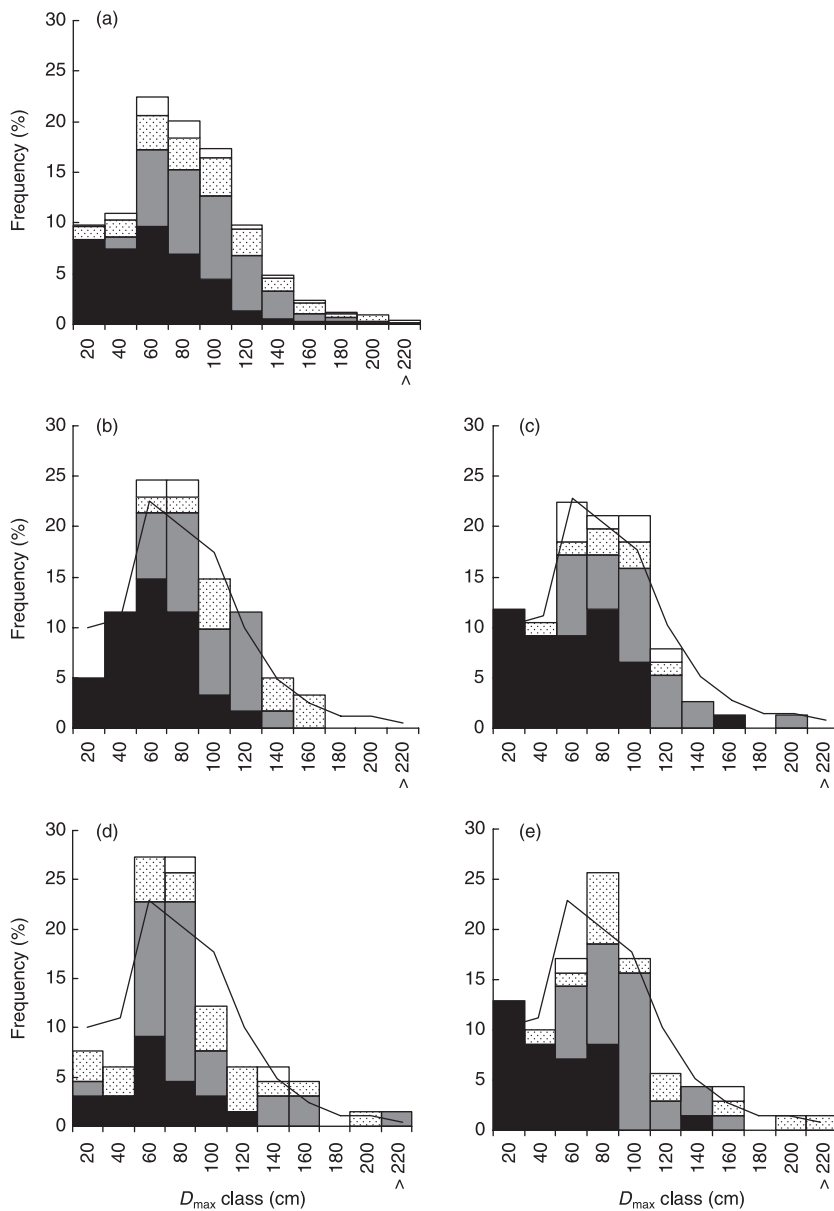


Fig. 1. Relative frequency distribution of maximum species diameters in different tropical forest communities. (a) Average for all 44 reserves, (b) forest with low annual rainfall (1268 mm) and low %pioneers (6.9%, Pra Suhien FR), (c) forest with high rainfall (1961 mm) and low %pioneers (5.7%, Fure Headwater FR), (d) forest with low rainfall (1377 mm) and high %pioneers (20.4%, Bia North), (e) forest with high rainfall (1677 mm) and high %pioneers (14.2%, Esukawkaw FR). Stacked bars are shown for shade bearers (black), non-pioneer light-demanders (dark grey), pioneers (dotted), and species with unknown regeneration guild (white). The continuous line represents the average frequency distribution of maximum species diameters of all 44 reserves. Note that trees < 5 cm d.b.h. were not included in this survey, and that species between 5 and 30 cm d.b.h. are relatively under represented because they were sampled in a smaller area.

of size classes should equal the square root of the number of observations (in our case we used a slightly larger number of classes (11) than recommended based on the square root of the average number of 65 species (8)). The classes had 20 cm width, with the exception of the first (5–20 cm d.b.h.) and the last (> 200 cm d.b.h.). We compared the observed frequency distribution of D_{\max} with the average frequency distribution of the 44 reserves.

Parameters that describe the size structure of the community (S_0 , S_{50} , S_{100} , S_{range} , the proportion of small species in the 5–20 cm size class, the proportion of species in the 180–200 cm size class) were related to rainfall and the pioneer index using Pearson correlations. %pioneers was \log_{10} -transformed prior to all statistical analyses. We note that reserve level data on rainfall and the $\log_{10}(\% \text{pioneers})$ are negatively correlated ($r = -0.66$, $P < 0.001$, $n = 44$), indicating that drier forests tend to have more pioneers (see also Hawthorne 1996). We therefore did a multiple forward regression to unravel whether rainfall and $\log_{10}(\% \text{pioneers})$ had a significant and independent effect on the size distribution parameters.

Results

SIZE DISTRIBUTION OF SPECIES

The average D_{\max} distribution of locally common Ghanaian tree species followed an approximately normal distribution, with a peak between 40 and 100 cm d.b.h. (Fig. 1a), a moderate number of species of small stature, and was skewed to the right with a low number of species of large stature. Of the 44 forest communities, 32 showed a normal distribution of D_{\max} of the more common tree species, 5 log-normal distribution and 7 communities another type of distribution (Kolmogorov–Smirnov test for (log)-normality, $P < 0.05$). The tree communities of a forest reserve may follow the average D_{\max} distribution (Fig. 1c), or have a relative paucity of small (Fig. 1d) or large (Fig. 1b) species. We found no evidence for a bimodal or multimodal distribution in any of the 44 forest reserves.

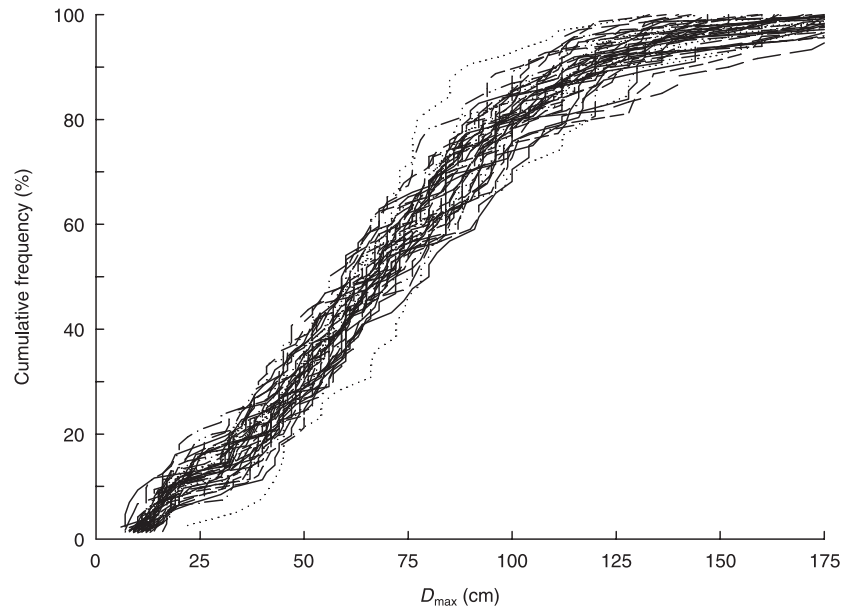


Fig. 2. Cumulative distribution function for the number of species in each 20 ha forest community plotted against maximum d.b.h. (D_{\max}) of those species. Each line represents a different forest community ($n = 44$).

Table 1. Pearson correlation between size structure of species communities, rainfall (Rain, $n = 41$), and %pioneers (%Pioneers, $n = 44$). In the right five columns the results of a multiple forward regression of variables on rainfall and %pioneers are shown; standardized regression coefficients (b), P -levels (P), and coefficients of determination (r^2). %Pioneers was \log_{10} -transformed prior to analysis. Results are given for the smallest (S_0), median (S_{50}) and largest (S_{100}) stature species in the community, the size range ($S_{\text{range}} = S_{100} - S_0$), the species packing (number of species/size range) and the skewness or asymmetry of the size distribution. A positive skewness indicates a larger tail of larger (rather than smaller) species, and a negative skewness a larger tail of smaller (rather than larger) species. Class₅₋₂₀ refers to the proportion of small species in the diameter size class of 5–20 cm, Class₁₈₀₋₂₀₀ to the proportion of species in the diameter size class of 180–200 cm

Variable	Rain		%Pioneers		Rain		%Pioneers		r^2
	r	P	r	P	b	P	b	P	
S_0	-0.07	NS	0.12	NS	–	NS	–	NS	–
S_{50}	-0.21	NS	0.24	NS	–	NS	–	NS	–
S_{90}	-0.58	***	0.59	***	-0.58	***	–	NS	0.34
S_{100}	-0.50	***	0.57	***	–	NS	0.54	***	0.30
S_{range}	-0.49	***	0.55	***	–	NS	0.53	***	0.28
Class ₅₋₂₀	0.27	NS	-0.14	NS	–	NS	–	NS	–
Class ₁₈₀₋₂₀₀	-0.41	**	0.44	**	–	NS	0.42	**	0.17
Skewness	-0.52	***	0.38	**	-0.52	***	–	NS	0.27
Residuals	0.15	NS	-0.29	NS	–	NS	–	NS	–
Species number	0.66	***	-0.62	***	0.38	*	-0.43	**	0.53
Species packing	0.73	***	-0.74	***	0.41	**	-0.48	***	0.66

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS $P > 0.05$.

Forest communities differed considerably in their D_{\max} distribution, especially for the larger size classes (Fig. 2); the median species D_{\max} (S_{50}) varies from 58 to 80 cm d.b.h. between the communities, and the 90th percentile of species size (S_{90}) varies from 95 to 158 cm d.b.h.

SIZE DISTRIBUTION VS. RAINFALL AND DISTURBANCE

Size range

The minimum (S_0) (Fig. 3a,b) and median (S_{50}) species size did not vary with rainfall or %pioneers (Table 1). However, the 90th percentile (S_{90}) and maximum species size (S_{100})

decreased significantly with an increase in rainfall and increased with higher %pioneers (Table 1, Fig. 3a,b). To check how the species size range is determined by the smallest and largest species in the community, we carried out a multiple regression of 44 size ranges on S_0 and S_{100} . The standardized regression coefficient for S_{100} is 1.00 ($P < 0.001$), and for S_0 is -0.01 ($P < 0.001$), indicating that both have a significant effect on the size range, but that the size range depends mostly on the largest species. The species size range therefore followed a similar pattern as S_{100} , showing a decrease with increasing rainfall and an increase with higher %pioneers. This can also be seen in Fig. 3a,b as the difference between the regression lines for S_0 and S_{100} .

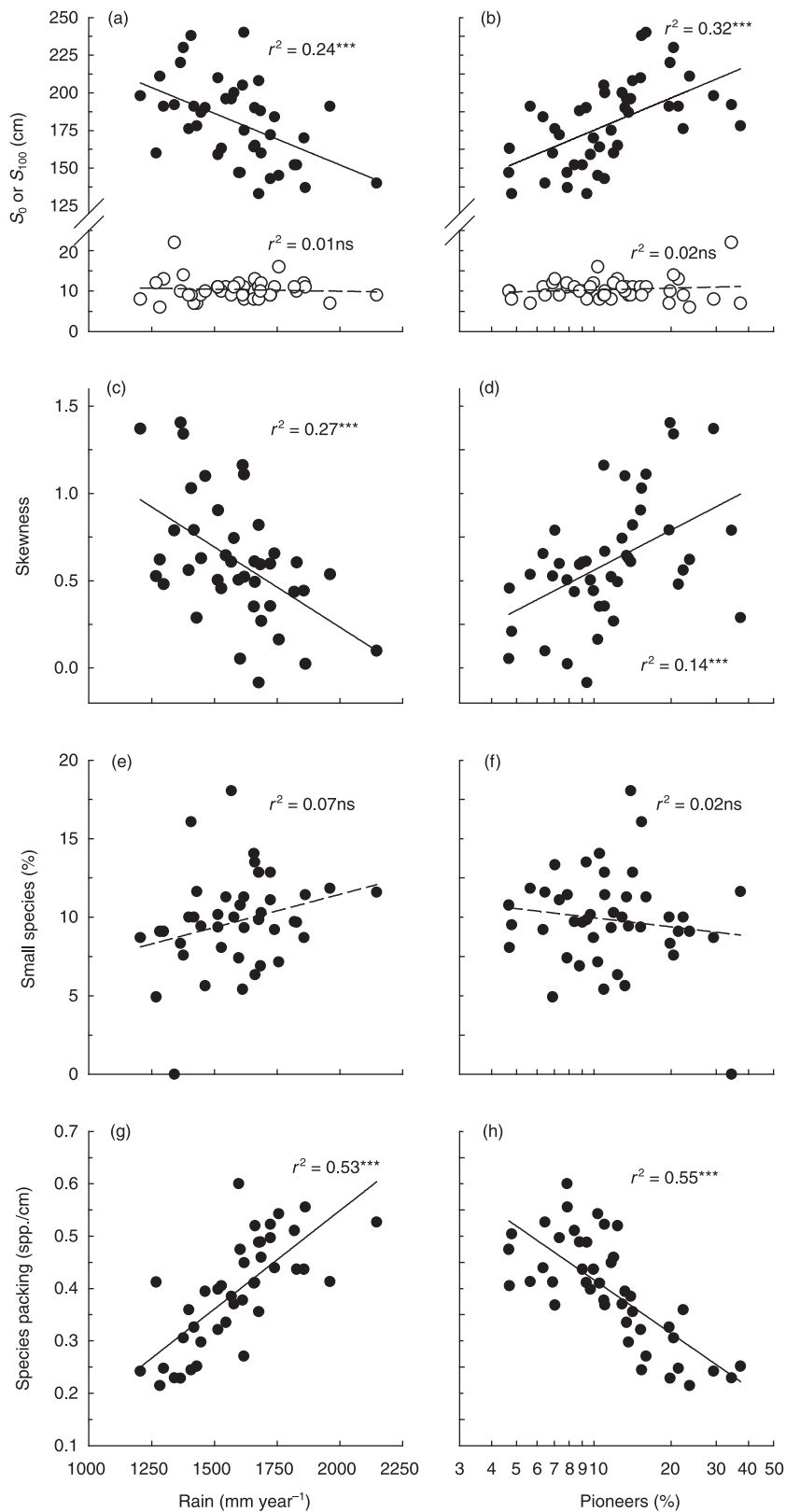


Fig. 3. Relationship between size structure of 44 tropical tree communities, annual rainfall (left panels), and %pioneers (right panels). (a, b) the smallest (S_0 , open symbols) and largest (S_{100} , filled symbols) maximum diameter of species in the community, (c, d) skewness of size distribution, (e, f) small species (% of species in the 5–20 cm d.b.h. class interval), (g, h) species packing (number of species/species diameter size range of the community). Regression lines, coefficients of determination, and significance levels are shown. Non-significant relationships are indicated with broken lines. Note that the %pioneers axis is log-transformed. NS: $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Proportion of small species

The size distribution of each community can also be described by the proportion of small species (5–20 cm d.b.h.) and large

species (180–200 cm d.b.h.) in the community, and by the skewness. The proportion of small-tree species did not vary significantly with rainfall or %pioneers (Table 1, Fig. 3e,f). On the other hand, the proportion of large-tree

species decreased significantly with an increase in rainfall, and increased with higher %pioneers (Table 1). Nearly all communities had a positive skewness, indicating a tendency for a D_{\max} distribution with a tail of large species. The skewness relationships thus follow the same pattern as the proportion of large species, and decreased with an increase in rainfall (Fig. 3c) and increased with higher %pioneers (Fig. 3d).

Species packing

Species packing was defined as the number of species (those with at least 10 individuals recorded in each forest sample) divided by the minimum-to-maximum size range of these species. A multiple regression showed that species packing is equally determined by species richness (standardized regression coefficient $b = 0.61$, $P < 0.001$) and size range ($b = -0.65$, $P < 0.001$). Species richness increased significantly with an increase in rainfall and decreased with the %pioneers. Species packing varied threefold between communities, ranging from 0.2 to 0.6 species cm^{-1} increase in diameter. Species packing increased strongly with rainfall (Fig. 3g) and decreased with %pioneers, at least when %pioneers reached 10% or more (Fig. 3h).

We used a forward multiple regression analysis to evaluate the relative contribution of rainfall and %pioneers to the size structure of the community. In two cases (S_{90} and skewness) rainfall was the only factor explaining significant amounts of variation in size structure, and in three cases (S_{100} , S_{range} , and the proportion of large species) %pioneers was the only factor explaining size structure (Table 1). In two cases both variables were important; both the species richness and species packing increased with an increase in rainfall and decreased with a higher %pioneers (Table 1).

Discussion

The size distribution of Ghanaian forest species was normal to log-normal. Size distributions varied strongly from community to community. We evaluated three aspects of size distribution (size range, proportion of small species, species packing) that have important consequences for resource partitioning and species richness. Variation in size structure was significantly related to environmental gradients in rainfall and disturbance, but not as we had predicted.

SIZE DISTRIBUTIONS OF SPECIES

The D_{\max} distribution of Ghanaian forest species generally shows a continuous, normal or log-normal distribution (Fig. 1). In contrast, Scheffer & van Nes (2006) suggested that size distributions of coexisting species should be discontinuous and multimodal. In their model, competition between coexisting species would lead to clusters of similar-sized species over the course of time, as species should be either sufficiently similar or sufficiently different to coexist. However, of the 44 tropical tree communities 32 showed a normal size distribution, 5 log-normal size distribution and for the 7 communities that

departed from (log)-normality, none showed evidence for a discontinuous bi- or multimodal size distribution. In fact, in many speciose tropical tree genera adaptive radiation has produced apparently continuous differences in their maximum size (Thomas 1996; Davies & Ashton 1999).

Interestingly, the species of temperate deciduous forests may show a marked bi-modal size distribution, with a small group of understorey species and a large group of canopy species (King *et al.* 2006). Terborgh (1985), proposed an explanation of such layering based on the vertical light profile in the forest canopy. In temperate forests, direct light can penetrate through gaps between adjacent tree crowns. At a certain distance below the canopy the sunflecks from different gaps between tree crowns overlap during the day, leading to a forest stratum with high spatially homogeneous light levels. It is in this stratum where typical forest understorey species like *Cornus* and *Cercis* attain their maximum height. Hence, layering of species in different forest strata may also result in a layering of trees in the stand (cf. King *et al.* 2006). Terborgh (1985) predicted that in the tropics the vertical light distribution and forest layering might be more continuous, as high sun angles and shallow canopy crowns allow for a more gradual and more even penetration of light.

The D_{\max} distribution of Ghanaian forest species showed a peak between 40 and 100 cm d.b.h., comprising mostly canopy species, along with a few subcanopy species. It is appealing to conjecture that this abundance of large species results from an evolutionary race, driven by asymmetric competition for light, in which the maximum height of the canopy is set by levels of water and nutrient availability (cf. Givnish 1988; Falster & Westoby 2003), or reproductive- and/or disturbance-based trade-offs (Kohyama 1993; Sheil *et al.* 2006). However, various factors have influenced our result.

The preponderance of large species in part reflects our sampling design, in which smaller trees were sampled at a lower intensity, and trees below 5 cm were excluded, thus underestimating the presence of small species. In rain forests in Sri Lanka, Ecuador and Panama, where a complete inventory of all size classes has been made (Gunatilleke *et al.* 2004; Valencia *et al.* 2004), shrubs and treelet species that attained maximum 10 m height made up as much as 30–38% of the woody species in the community. In DR Congo 34% of all tree species that could attain 1 cm diameter did not exceed 10 cm diameter (Makana *et al.* 2004). Thomas (2003) evaluated the maximum height distribution of all species in a lowland dipterocarp forest in Pasoh, Malaysia, in which species down to 1 cm d.b.h. were included. He found a peak of subcanopy species between 20 and 30 m height, whereas the canopy was between 30 and 40 m height. For four other tropical forests the peak was also between 20 and 30 m height (King *et al.* 2006). This raises the question why there are so few emergent species, given that they occupy the best position in the vertical light profile in the forest canopy (cf. Aarssen *et al.* 2006). Probably the high irradiance is accompanied by an increased risk of mechanical failure due to strong winds, a longer time before reproductive size is achieved, and trade-offs with the competitive abilities of seedlings and saplings when

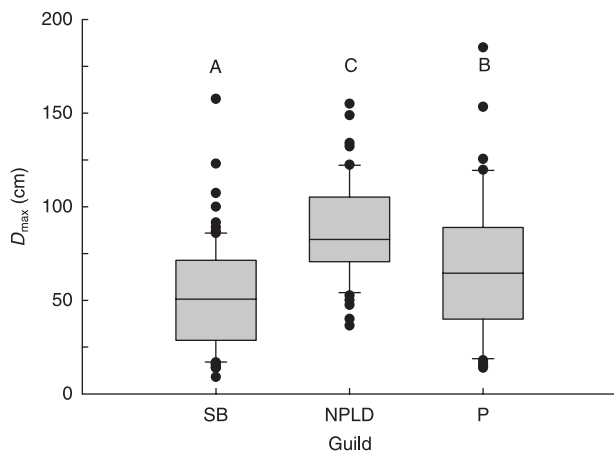


Fig. 4. Boxplot of the maximum diameters (D_{\max}) of shade-bearing (SB, $n = 85$), non-pioneer light demanding (NPLD, $n = 56$) and pioneer (P , $n = 47$) species. For species that occurred in several forest reserves, the average maximum diameter across the 44 forest reserves is used. The lower, middle, and upper part of the boxplot indicate the 25th, 50th and 75th percentile of D_{\max} , the lower and upper bar the 10th and 90th percentile, respectively. Dots represent outliers. The guilds differ significantly in their D_{\max} (ANOVA, $F_{2,182} = 17.2$, $P < 0.001$). Guilds that differ significantly in their D_{\max} are indicated by a different letter (Student-Newman Keuls post-hoc test, $P < 0.05$).

confronted with small stature taxa in low light understory environments (Kohyama 1993; Thomas & Bazzaz 1999; Sheil *et al.* 2006). In that sense the best compromise would be represented by canopy species that take advantage of full light on their crowns, while avoiding the risk of becoming too exposed, and needing less time to attain their reproductive size. Alternatively, productive site conditions and low disturbance regimes are so rare in nature, that the emergent species that specialize for those conditions are also rare (Aarssen *et al.* 2006).

SIZE RANGE

We conjectured that the size range would increase with an increase in rainfall because higher water availability leads to more productive conditions with larger and thicker trees, and hence a larger size range. In this section, we interpret size mostly in terms of height, although we acknowledge that species and forest types may vary in their height at a given d.b.h. (e.g. Poorter *et al.* 2003). The size range was mostly determined by the largest species in the community. Maximum tree size, the proportion of large trees, skewness and size range decreased with an increase in rainfall (Table 1, Fig. 3a,c), in contrast to the hypothesis. The fact that maximum tree size decreased with rainfall suggests that factors other than hydraulic limitation set an upper limit on maximum tree height (Koch *et al.* 2004). An obvious hypothesis is that forest size, and hence productivity, is determined by nutrient availability as well as moisture (cf. Huston 1980). In Ghana, forest stature increases from dry deciduous forests (800 mm year^{-1}) to moist semi-deciduous forests ($1400 \text{ mm year}^{-1}$) halfway along the rainfall gradient before declining again in the wettest sites

($2100 \text{ mm year}^{-1}$) which possess leached, nutrient-poor soils (Hall & Swaine 1981). The tallest forests are believed to attain their stature because both water and nutrients are more favourable than in either the wetter (low nutrient) or drier (low moisture) sites (Hall & Swaine 1981). In the current study, we have focused on the wetter part of the gradient (1200–2100 mm). This may explain why we found a negative relationship between size range and rainfall. Another reason might be that with the increase in rainfall, and thus higher productivity, light competition increases as well, resulting in taller and more slender (rather than thicker) trees.

We conjectured that size range would decrease with the %pioneers because a high disturbance regime prevents species from attaining their maximum size and favours small species. However, the data suggest an increasing relationship between size range and the %pioneers (Fig. 3b). West African forests are perhaps unusual in possessing a high number of especially large pioneer species (Turner 2001) that dominate the canopy (van Gernerden *et al.* 2003). The maximum species sizes may indeed be reduced once disturbance becomes too frequent or severe, but maximum species sizes increase from low to moderate %pioneers.

PROPORTION OF SMALL SPECIES

We predicted that the proportion of small species would increase with rainfall because longer growing seasons permit increased shade tolerance, allowing more specialisation amongst understory species. Yet, in our analysis the proportion of species of small stature (with 10 or more stems) was not significantly related to rainfall (Table 1). We predicted that the proportion of small species would increase with higher %pioneers because disturbed areas are either colonized by small, short-lived pioneer species or because colonization has been too recent for the species to attain their maximum size. We found no evidence for such a relationship (Fig. 3f). Maybe this is because small, short-lived pioneers that regenerate after heavy disturbance are indeed quite common, but in Ghana there are many larger, long-lived pioneers as well, resulting in a wide spread of maximum diameters within the pioneer guild (Fig. 4), and an average maximum species diameter of pioneers that was larger than those of shade bearers – at least amongst relatively common and widespread species. These large, long-lived pioneers are usually abundant alongside smaller pioneer species (Fig. 1) from the first stages of succession, including canopy (e.g. *Terminalia* spp.) or emergent species (e.g. *Lophira alata*, *Triplochiton scleroxylon*, *Ceiba pentandra*) (Hawthorne 1993; Turner 2001; Poorter *et al.* 2006). In addition, even when smaller pioneers are prevalent, dominance by a small number of species is common (van Breugel *et al.* 2007) so they may be represented by only a few species. Furthermore the %pioneers indicates whether disturbances have resulted in open sites that could be colonized by pioneers. It does not capture, however, the impact of disturbance on the remnant forest mass. Different types of disturbances may have different effects on the size structure of the plant community. Ground fires, for example, preferentially

kill off trees in the smallest size classes, leading to a reduction of small understorey species (Hawthorne 1994; van Nieuwstadt & Sheil 2005), whereas logging targets larger trees.

SPECIES PACKING

Species richness and size range contribute equally to partitioning of the light gradient by different tree species (species packing). Species packing was predicted to increase with an increase in rainfall as the absence of seasonal drought stress may lead to a higher degree of specialization, and hence, more densely-packed species. This prediction was supported by the data, which showed a strong positive relationship between packing and rainfall (Fig. 3g). Similarly, a positive relationship between rainfall and size-based species packing has also been observed for African herbivore communities (Prins & Olff 1998). The question remains whether the absence of drought stress alone causes a higher degree of specialization, as many factors may contribute to higher species richness in the wet tropics (Wright 2002), such as slow competitive exclusion through dispersal limitation, and distance- and density-dependent mortality by pests and pathogens.

Species packing was predicted to decrease with higher %pioneers, as a high disturbance regime prevents the community from being fully saturated, leading to lower species richness and less species packing. This prediction was supported by the data (Fig. 3h), and even held when the effect of rainfall on packing was taken into account (Table 1). Disturbance therefore, not only physically increases the number of open sites where species can establish, but also creates niche opportunities ('gaps') along the size gradient. And it is especially these open niches in the size distributions that are filled up by new species that establish in the community, because they have the appropriate size to occupy this niche (Allen *et al.* 1999).

Hutchinson (1959) suggested that pairs of animal species can only coexist in a stable system if they are sufficiently different, and found a size ratio of 2 between the logarithm of body mass of species that are consecutive in rank size. We are not aware of any studies that have evaluated such size ratios for plants. Using allometric equations that relate biomass to d.b.h. (Chave *et al.* 2005), we found an average log 'body mass' ratio of 1.020 (range 1.012–1.035) for the 44 Ghanaian tree communities. This ratio is considerably smaller than observed for animal species. Plants may have smaller size ratios because competition for light is local and asymmetric, whereas competition amongst animals is more diffuse and symmetrical. Plants may therefore escape competition with similar-sized species through segregation in space (e.g. small pioneers may escape from competition in the understorey by establishing in disturbed sites; Kohyama 1993), time (e.g. by establishing in a different successional phase; Falster & Westoby 2005), or both space and time (Aubréville 1938).

Conclusions

Tree species size distributions of Ghanaian tropical forest communities were continuous and (log)-normal, and did not

reveal clusters of similar-sized species, as predicted by the self-organized similarity theory of Scheffer & van Nes (2006). Nor did these forests show the disjunct species layering seen in temperate forests, thus potentially contributing to species packing and higher species diversity in tropical forests. Also within Ghanaian tropical forests there was substantial variation in size structure of communities. Multiple regression analysis showed that this variation was sometimes related to rainfall, and sometimes related to disturbance. Size distributions in wet forests were less skewed, with a smaller proportion of big species and a smaller size range. At the same time they had higher species richness, resulting in tighter species packing.

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