

REPORT

Tree size frequency distributions, plant density, age and community disturbance

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Abstract

We show that explicit mathematical and biological relationships exist among the scaling exponents and the allometric constants (α and β , respectively) of log–log linear tree-community size frequency distributions, plant density N_T , and minimum, maximum and average stem diameters (D_{\min} , D_{\max} , and \bar{D} , respectively). As individuals grow in size and D_{\max} increases, N_T is predicted to decrease as reflected by a decrease in the numerical value of α and an increase in the value of β . Our derivations further show that N_T decreases as \bar{D} increases even if D_{\min} or D_{\max} remain unchanged. Because D_{\max} and the age of the largest individuals in a community are correlated, albeit weakly, we argue that the interdependent relationships among the numerical values of α , β , N_T , and \bar{D} shed light on the extent to which communities have experienced recent global disturbance. These predicted relationships receive strong statistical support using two large datasets spanning a broad spectrum of tree-dominated communities.

Keywords

Allometry, community ecology, plant size, stem diameter.

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INTRODUCTION

Static stem size or age distributions provide useful insights into many important macroecological phenomena, although they cannot be used to accurately assess or predict community growth or health (Enright & Watson 1991; Condit *et al.* 1998; Chave 1999; Kelly & Bowler 2002). For example, across a broad spectrum of indigenous tree-dominated communities, stem size frequencies for 0.1 ha sample areas are reported to be log–log linear and to scale, on average, as the -2 power of stem diameter, indicating that the capacity to fill space does not statistically vary across these otherwise ecologically diverse community samples (Enquist & Niklas 2001). Because species numbers vary across three orders of magnitude, the ‘average’ -2 scaling exponent also indicates that, on average, the capacity to occupy space varies little with respect to community species composition, i.e. the ability to fill space as gauged by stem size frequency distributions appears equally well achieved either by many small or a few large individuals, or by any intermediate size-composition, regardless of species number or composition (Enquist & Niklas 2001).

Nevertheless, the scaling exponents reported for these communities also vary significantly, indicating that some community structures fail to occupy available space, whereas

others are composed of densely packed individuals. A number of biological and physical factors may account for these statistical ‘outliers’, e.g. site-specific resource availability and limitation, unique species compositions, mortality-recruitment regimes, and duration, periodicity, and magnitude of disturbance (see Enright & Watson 1991; Roberts & Gilliam 1995; Condit *et al.* 1998; Chave 1999; Kelly *et al.* 2001; Kelly & Bowler 2002; Stevens & Carson 2002). The influence of these factors on size frequency distributions nevertheless remains problematic in part because the mathematical relationships among the various parameters that describe the ‘shape’ of size distributions have not been fully explored (see McGeoch & Gaston 2002).

Here, we show how the numerical values of the scaling exponents, allometric constants and other parameters that define the ‘shapes’ of size frequency distributions mathematically and biologically interrelate with respect to other important community properties, such as the number of individuals per unit area (plant density). Specifically, we provide explicit equations that predict plant density and average stem diameter based on the numerical values of the scaling exponents and allometric constants of community log–log size frequency distributions (i.e. the slopes and intercepts, respectively). These predictions are empirically examined and statistically verified using two large datasets

spanning a broad spectrum of tree-dominated communities. We also present circumstantial evidence that average as well as maximum stem diameter is correlated with the age of these communities. Although size frequency distributions are influenced by complex and manifold factors, we nevertheless hypothesize that the ‘shape’ of these distributions reflects to some significant degree the extent to which species within communities have experienced comparatively recent physical or biological disturbance.

Size frequency distribution curves

Because stem diameter is easily measured and typically correlates well with other important ecological and phenotypic features, e.g. plant height, leaf area and lateral crown spread (for examples, see Niklas 1994), plant size frequency distributions are typically rendered as histograms and statistically described in terms of the regression curve that best approximates the numbers of individuals N_i in different basal stem diameter classes D_i . For statistical purposes, the protocol used to sort individuals into the different D_i requires a uniform bin size Δx . Operationally and statistically, the choice of Δx is limited by the size-structure of a particular distribution. For large datasets spanning many orders of magnitude of stem size and many individuals, large bin sizes may be used. But, as will be shown, the choice of Δx profoundly influences the statistical parameters describing the ‘shape’ of any size frequency distribution.

For many plant communities, especially those dominated by tree species, stem size histograms are statistically well described by the regression formula $N_i = \beta D_i^{-\alpha}$ (Fig. 1a), which is often expressed logarithmically as $\log N_i = \log \beta - \alpha \log D_i$ to emphasize that the ‘shape’ of a histogram is described by the numerical values of its slope (scaling exponent α) and its Y-intercept (the Log of the allometric constant β) (Fig. 1b). However, it is often unnoticed that the numerical values of α and β depend on the numerical value of Δx . Specifically, numerical simulations show that the numerical values of α and β increase as Δx increases. Thus, for a hypothetical size frequency distribution for 445 stems within the range of $1 \text{ cm} \leq D_i \leq 39 \text{ cm}$, ordinary least squares regression analysis of the \log_{10} -transformed data obtains $\alpha = -1.62$ and $\beta = 383.8$ (when $\Delta x = 2 \text{ cm}$), $\alpha = -1.76$ and $\beta = 1196$ (when $\Delta x = 4 \text{ cm}$), and $\alpha = -2.06$ and $\beta = 6248$ (when $\Delta x = 8 \text{ cm}$).

An additional caveat is that the log–log linear power-function $N_i = \beta D_i^{-\alpha}$ may not be statistically adequate for some frequency distributions, because the shape of a size frequency distribution is also influenced by community sample-areas (see McGeoch & Gaston 2002). Communities sampled over large areas (e.g. $\geq 50 \text{ ha}$ plots) can have log–log (concave) curvilinear rather than log–log linear distributions (see Chave 1999). This phenomenology may reflect the

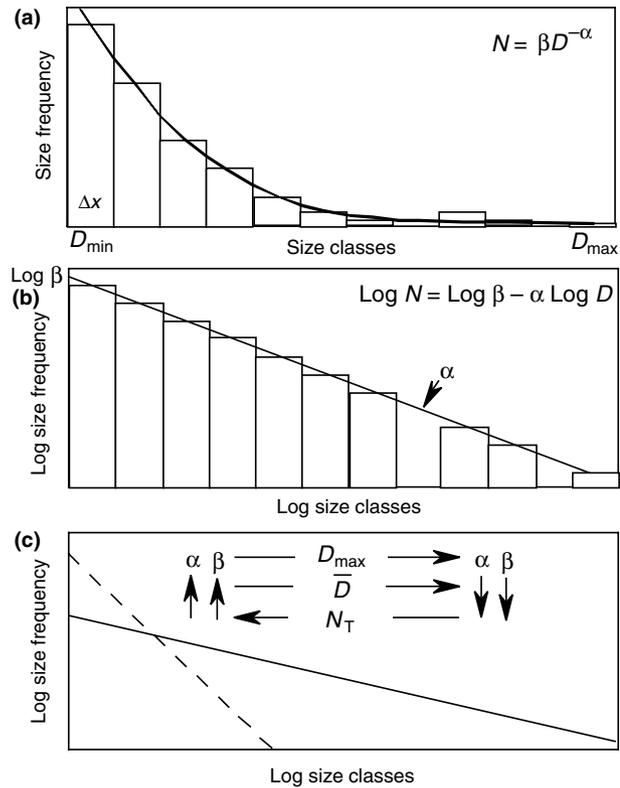


Figure 1 Stereotypical untransformed and log-transformed stem size (diameter) frequency distribution of a plant population or community. The untransformed and log-transformed distribution (a and b, respectively) is defined mathematically by the slope and Y-intercept of the regression curve (the scaling exponent α and the allometric constant β , respectively) and by minimum and maximum diameter (D_{min} and D_{max} , respectively). As a result of self-thinning and decreasing plant density N_T , the numerical values of α and β are expected to decrease (i.e. the slope of the regression curve is expected to decrease) as D_{max} and average stem diameter \bar{D} increase (c).

extent to which habitat heterogeneity or species diversity is represented in any particular community ‘sample’. However, departures from log–log linearity are not often observed for communities sampled over small areas (e.g. 0.1–1.0 ha plots) nor when these small data sets are combined to achieve continental or worldwide representations (see Enquist & Niklas 2001).

Provided that size frequency histograms are statistically adequately described by regression curves with the form $N_i = \beta D_i^{-\alpha}$, the relationship between total plant density (i.e. the total number of individuals per sample-area, N_T) and the statistical parameters describing a histogram is approximated by the formula

$$N_T = \frac{\beta}{\Delta x(1 - \alpha)} (D_{max}^{1-\alpha} - D_{min}^{1-\alpha}), \tag{1}$$

where D_{\max} and D_{\min} are the maximum and minimum stem diameter in the dataset, respectively. The term Δx is retained in eqn 1 to emphasize, once again, that α - and β -values are influenced by this parameter. Importantly, eqn 1 is an approximate estimate of N_T for a specified value of Δx , because it is based on the integral of $N_i = \beta D_i^{-\alpha}$ and thus assumes that D_i and N_i vary continuously, i.e. $N_T = \int_{D_{\min}}^{D_{\max}} (N/\Delta x) dD$, rather than in the step-wise manner of a size frequency histogram. The accuracy of eqn 1 also erodes as the number of unoccupied or statistically variant size classes increases. Note that as the value of Δx approaches zero, the number of unoccupied size class bins will increase. For the database used to assess our mathematical derivations (see The Gentry datasets), eqn 1 nevertheless appears to be remarkably accurate provided that Δx is held constant, i.e. linear regression of observed vs. estimated N_T obtains a slope of 1.01 within the range $500 \text{ ha}^{-1} \leq N_T \leq 10\,000 \text{ ha}^{-1}$. However, for higher plant densities, eqn 1 progressively overestimates N_T because of unoccupied stem size classes.

With these caveats in mind, eqn 1 predicts, at the level of an entire community, relationships that mimic those of self-thinning theory for monospecific even-aged populations. Specifically, self-thinning theory predicts that, over time, the number of smaller individuals in even-aged populations will decrease as the number of larger individuals increases (Yoda *et al.* 1963; White & Harper 1970; White 1980). Extensively thinned populations are thus expected to have size frequency distributions with lower α and β numerical values compared with those of less thinned populations (Fig. 1c). Likewise, D_{\max} will increase over time as some conspecifics mature and increase in size by the accumulation of primary or secondary tissues, just as predicted by eqn 1. Arguably, this similitude may reflect the fact that, regardless of many significant species-specific differences, most plants must perform the same basic biological tasks to grow and survive and that the simultaneous performance of these tasks has resulted in evolutionary convergence in terms of size-dependent efficiency (see Niklas 1997). It is nevertheless clear that communities consist of manifold populations of different species, each experiencing the potential effects of interspecific competition, intraspecific self-thinning, and demographic shifts resulting from progeny recruitment and mortality. Thus, the relationships depicted by eqn 1 reflect the sum interaction of numerous phenomena in terms of the relationship between total plant density and the 'shape' of the stem size frequency distribution (as defined by the numerical values of α and β).

In this regard, an additional important community feature is average stem diameter, which will increase as the size or number of the largest individuals in a community increases, or as the number of smaller individuals decreases. Because a community is composed of more than one species, a shift in

average stem diameter can result from changes in species composition or in demographic changes in the size structure of one or more persistent species. However, in either case, an increase in average stem size requires that some individuals in a community have time to mature and thus arguably reflects the propinquity or intensity of past disturbance levels.

It is easily shown that, for any community with a size distribution described by $N_i = \beta D_i^{-\alpha}$, average stem diameter \bar{D} is given by the formula

$$\bar{D} = \frac{\int_{N_{\min}}^{N_{\max}} D dN}{\int_{N_{\min}}^{N_{\max}} dN} = \frac{\int_{D_{\max}}^{D_{\min}} D \frac{dN}{dD} dD}{\int_{D_{\max}}^{D_{\min}} \frac{dN}{dD} dD} = \frac{\int_{D_{\max}}^{D_{\min}} D(-\alpha\beta D^{-\alpha-1}) dD}{\int_{D_{\max}}^{D_{\min}} (-\alpha\beta D^{-\alpha-1}) dD}$$

$$\bar{D} = \frac{(D_{\min}^{1-\alpha} - D_{\max}^{1-\alpha})}{(1 - 1/\alpha)(D_{\min}^{-\alpha} - D_{\max}^{-\alpha})}. \quad (2)$$

Combining eqns 1 and 2 and solving for N_T , we obtain the equation

$$N_T = \frac{\beta}{\alpha \Delta x} \bar{D} (D_{\min}^{-\alpha} - D_{\max}^{-\alpha}). \quad (3)$$

Once again, Δx is retained in this formula to emphasize the dependency of α - and β -values on this parameter. This last relationship draws attention to the complex interrelationships between plant density (and thus the extent to which space is occupied), average plant size (and thus arguably levels of recent disturbance), and the shape of the size frequency distribution as defined by α and β . Specifically, it predicts that plant density will decrease as maximum stem diameter increases or as the centroid of the size frequency distribution (defined by average stem diameter) shifts towards the larger stem diameter classes. These changes are necessarily attended by a decrease in the numerical value of β and by a progressively less negative α -value (Fig. 1c). The similitude between the predictions of eqn 3 and those of self-thinning theory are once again apparent, albeit for different reasons, i.e. population (community) plant density is expected to decrease as conspecifics (larger individuals drawn from two or more species) increase in size (as gauged by minimum, average, or maximum stem size).

At the community-level, shifts of the size frequency centroid are important for two reasons. First, theoretical treatments of community dynamics strive to identify the scaling relationship between plant density and plant size analytically, and second, even if minimum and maximum stem diameters vary little across communities, these dynamics are made manifest by changes in average stem diameter. The extent to which a community fills space simultaneously influences the numerical values of α , β , N_T , and \bar{D} . Therefore, no treatment of community species

'packaging' is mathematically or biologically complete until it addresses the explicit relationships among these important parameters. As noted, community-level responses to inter-specific crowding or disturbance are far more complex than those of monotypic populations. Nevertheless, we believe that the simultaneous response of a community as a whole to crowding and 'global' disturbance can be gauged, albeit indirectly on the basis of its average as well as its maximum plant size.

The Gentry datasets

To test the foregoing predictions, we used the community size class distributions calculated for the Gentry database (see Enquist & Niklas 2001). This database is available online (at <http://www.mobot.org/MOBOT/research/gentry/welcome.shtml>) and in published form (Phillips & Miller in press). For each of 226 communities, Gentry gives the species identification and the number and diameter for all (liana and self-supporting monocot and dicot) stems measuring ≥ 2.54 cm in diameter (at breast height d.b.h., but not necessarily above buttress height) within 10 closely spaced transects each measuring 2×50 m in area (total sampled area per site = 0.1 ha). This database may not be representative of all forested communities. Gentry is reported to have selected sites in a nonsystematic manner biasing in favour of species-rich samples (J. Miller, pers. comm.). Nevertheless, the datasets span three orders of magnitude in plant density and species number, and represent a worldwide compendium gathered by one individual. As such, it permits comparisons across (largely closed canopy) communities that vary significantly in size frequency distributions, plant density, species composition and geographic location.

All size class distributions were determined using a 2 cm bin size, because consistency in bin size is required to compare α - and β -values across sites (see eqns 1–3 and comments regarding Δx ; see also Enquist & Niklas 2001). Bins with fewer than five individuals were excluded. However, the values reported here for D_{\max} are those of the largest individuals reported by Gentry for each site. The exclusion of bins with fewer than five individuals necessarily fails to capture the effects of the full stem size range for each site because the largest individuals are typically few in number. To evaluate this concern, we randomly selected 50 Gentry sites and assessed whether the inclusion of individuals in all bin sizes, regardless of their number, significantly affected the numerical values of α or β when bin sizes with five or fewer individuals are excluded. We also assessed whether \log_{10} - \log_{10} nonlinear regression curves provide a better fit to the data than \log_{10} - \log_{10} linear approximations.

Across these 50 communities, the inclusion of individuals from all bin sizes had little or no statistically significant

affect on the numerical values of α or β (based on t -test comparisons and parameter 95% confidence intervals) because bin sizes containing five or fewer individuals are few in number per site and because the total number the individuals in these excluded bin sizes is small in comparison with the number of individuals in the other bin sizes. Also, nonlinear regression-curve models did not provide a better fit for the Gentry datasets, once again, because the total number of individuals in excluded bin sizes is small in comparison with total community plant number. Exceptions to these findings were communities with $N_T < 100$, which account for $< 3\%$ ($n = 6$) of the total number of sites in Gentry database (see Fig. 3).

In this regard, we also point out that our objective here is to explore the relationships among α , β , D_{\max} and N_T in terms of the predictions of eqns 1–3, which assume that size frequency distributions are, on average, described by the formula $N_i = \beta D_i^{-\alpha}$. Likewise, the exclusion of bin sizes with less than or equal to five individuals provides a direct comparison between the results reported here and those presented in another study of the same database using the same bin-exclusion protocol (see Enquist & Niklas 2001). For these reasons, we believe that the protocols used to determine α and β are statistically legitimate and conceptually justified. Thus, for the data presented here, regression of \log_{10} -transformed N_i against \log_{10} -transformed D_i was used to determine the α - and β -values for each of the Gentry sites. The same regression protocol was used to determine the statistical relationships across communities among N_T , α , β , D_{\min} , D_{\max} and \bar{D} .

With these caveats in mind, our analyses of the Gentry database indicate that the numerical values of α , β , D_{\max} , and N_T are correlated across all communities in ways that are consistent with the predictions emerging from eqns 1–3. As expected (see Fig. 1c), the numerical value of α increases as the value of β increases ($r^2 = 0.889$, $F = 1780$, $P < 0.0001$) (Fig. 2a). Across the same datasets, the numerical values of α and β decrease as D_{\max} increases ($r^2 = 0.363$, $F = 125.7$, $P < 0.0001$ and $r^2 = 0.261$, $F = 78.9$, $P < 0.0001$, respectively) (Fig. 2b,c). Likewise, the values of β and α increase as N_T increases ($r^2 = 0.638$, $n = 226$, $F = 394.4$, $P < 0.0001$ and $r^2 = 0.469$, $F = 195$, $P < 0.0001$, respectively) (Fig. 3a,b).

The relationship between maximum stem diameter and plant density is less clear statistically in part because maximum stem diameter spans only two orders of magnitude. As a result, D_{\max} varied little with respect to N_T ($r^2 = 0.021$, $P = 0.231$). However, visual inspection of the bivariate plot of D_{\max} vs. N_T shows that, on average, D_{\max} and N_T are inversely correlated (Fig. 3c). More important, average stem diameter \bar{D} (computed on the basis of eqn 2) increases with increasing maximum stem diameter ($r^2 = 0.350$, $F = 119$, $P < 0.0001$) and decreasing

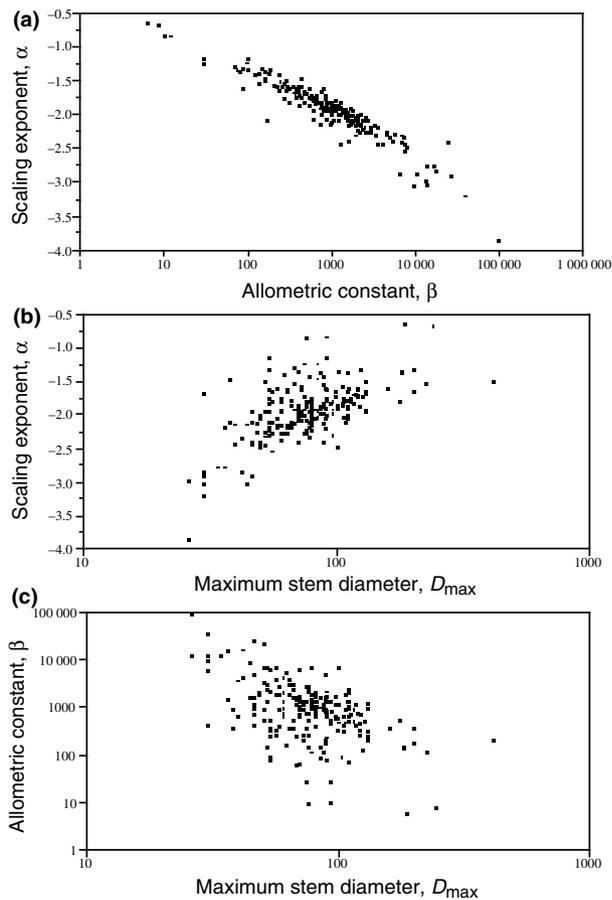


Figure 2 Relationships among the slopes and Y -intercepts of the regression curves (the scaling exponent α and the allometric constant β , respectively) of stem size frequency distributions and maximum stem diameter D_{\max} (units in cm) across the Gentry data sets. See text for additional details.

plant density ($r^2 = 0.520$, $F = 239$, $P < 0.0001$) (Fig. 4a,b). Across all communities, the slope of the ordinary least squares regression curve for $\log_{10} \bar{D}$ vs. $\log_{10} N_T$ is -0.33 (SE ± 0.02 ; 95% CI = -0.37 to -0.29). Thus, average stem diameter scales as the $-1/3$ power of plant density.

To test the reliability of computed \bar{D} values, average stem diameter was determined directly for 17 selected datasets randomly selected from Africa, North America, South America and Meso-America. Linear regression of the actual vs. estimated \bar{D} values (using eqn 2) obtains a slope of 0.93 ($r^2 = 0.852$, $F = 86.1$, $P < 0.0001$), which provides evidence that eqn 2 gives reasonably accurate estimates of \bar{D} .

The inverse relationship between \bar{D} vs. N_T observed for the Gentry datasets is also consistent with the statistical structure of another large compendium for standing tree biomass (Cannell 1982). For these data, the slope of the ordinary least squares regression curve of $\log_{10} \bar{D}$ vs. \log_{10}

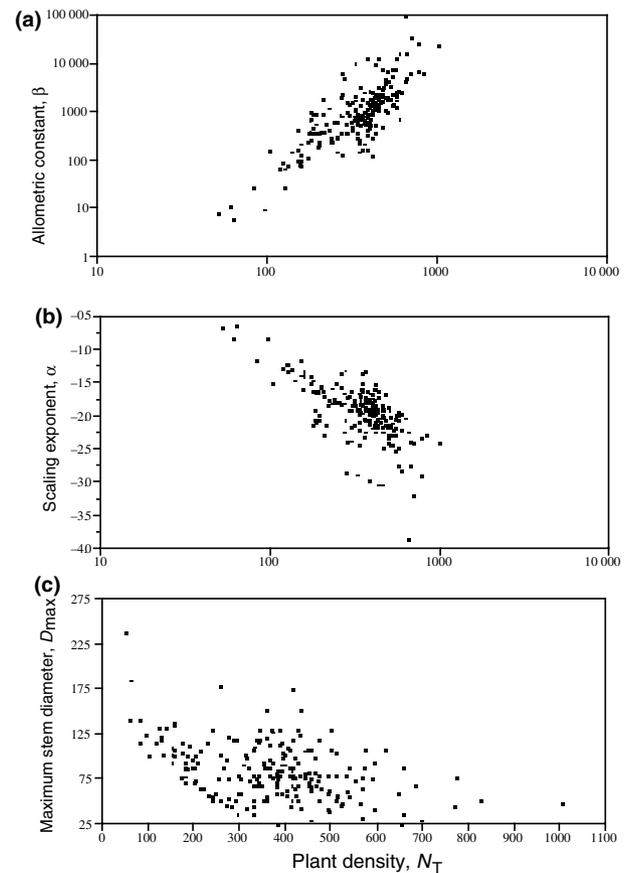


Figure 3 Relationships among the slopes and Y -intercepts of the regression curves (the scaling exponent α and the allometric constant β , respectively) of stem size frequency distributions, maximum stem diameter D_{\max} (in cm) and plant density N_T (plants per 0.1 ha) across the Gentry datasets. See text for additional details.

N_T is -0.53 (SE ± 0.01 ; 95% CI = -0.56 to -0.51 , $r^2 = 0.626$, $n = 344$, $F = 572$, $P < 0.0001$) (Fig. 4c). For the Cannell datasets, average stem cross-sectional area \bar{A}_S was calculated by dividing total stand basal stem cross-sectional area by N_T and average plant diameter was then calculated using the formula $(4\bar{A}_S/\pi)^{1/2}$. Although the methods used to compute average stem diameter differ, the same trend nevertheless exists, i.e. \bar{D} is observed to increase as N_T decreases as predicted by eqn 3.

Finally, to determine the contribution of the largest (and presumably oldest) individuals to total community standing size, we determined total community basal stem area TBA for each of the Gentry data sets and calculated the total basal area of the four largest individuals $tba4$ in each community. Linear regression of $tba4$ vs. TBA obtains a slope of 0.336 ($r^2 = 0.474$, $F = 107.3$, $P < 0.0001$). The four largest individuals contribute, on average, 26.6%

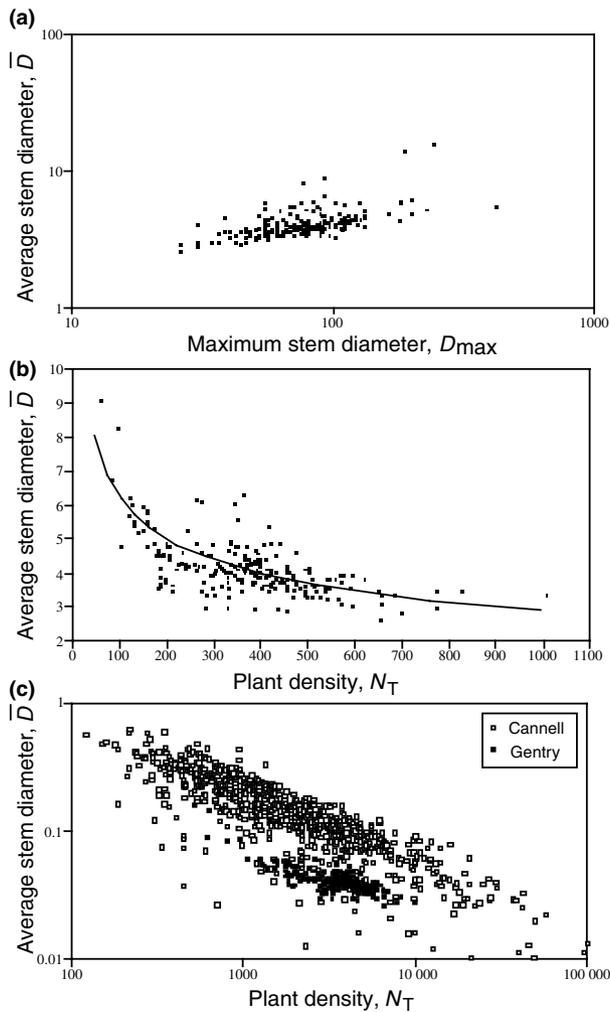


Figure 4 Relationships among the average \bar{D} and maximum stem diameter D_{\max} (units in cm) and plant density across N_T (units in plants per 0.1 ha) across the Gentry datasets (a and b) and between the Gentry and Cannell datasets (c). Average stem diameter for the Gentry datasets was computed based on eqn 2 (see text); average stem diameter for the Cannell datasets was computed based on the quotient of total basal stem area and plant density (units in m and 1.0 ha). Values of \bar{D} and N_T for the Gentry datasets have been adjusted to reflect differences in original units (cm vs. m) and sample areas (0.1 ha vs. 1.0 ha).

(SE \pm 1.34%) of the total basal area per community; for some exceptional (rare) communities, the percentage of contribution exceeds 70%.

DISCUSSION

We have shown how the ‘shape’ of community size frequency distributions (as defined by the numerical values of their scaling exponents α and allometric constants β) mathematically and biologically relates to total community

plant density and thus to the extent to which available physical space is collectively occupied by species. We have also shown how minimum, average and maximum stem diameter relate to plant density in conjunction with α - and β -values. A significant prediction emerging from these relationships is that the centroid of a size frequency distribution (defined by average stem diameter) can shift without a significant change in either community minimum or maximum stem diameter. Another prediction is that the centroid shifts towards larger individuals as total community plant density decreases (attended by a decrease in α - and β -values).

These properties of community size frequency distributions, which are substantiated empirically by our analyses of the Gentry database, are superficially similar to the behaviour of monospecific populations as predicted by self-thinning theory (Yoda *et al.* 1963; White & Harper 1970; White 1980). Indeed, we have drawn attention to the similarities between these two phenomenologies, both mathematically and biologically. It is nevertheless clear that communities do not ‘self-thin’ as do populations. The behaviour of a community reflects the cumulative responses (e.g. recruitment and mortality) of all of its constituent species, each of which may react to inter- and intra-specific packaging, competition and other factors differently. Thus, a reduction in plant density attended by a shift in the centroid of a community to the right of a size frequency distribution may reflect the elimination of small species or a reduction in their absolute numbers attended by the growth in size of coexisting species or the introduction of new species capable of reaching large size at maturity if undisturbed (for examples, see Condit *et al.* 1998; Kelly *et al.* 2001; Stevens & Carson 2002).

The inverse relationship between average stem diameter and plant density at the level of a community nevertheless remains interesting. Although minimum and maximum stem diameters vary comparatively little across the communities examined here, the diameter of an ‘average’ individual increases as population density decreases such that an increasing portion of total community size (as gauged by stem diameter or basal area) progressively resides in comparatively fewer large individuals. Our data indicate that the largest individuals in some of these communities can represent a significant fraction of total community basal stem area and thus biomass. We postulate that disturbance is one of the more likely explanations for this phenomenology. Arguably, woody species cannot achieve large size rapidly because this requires the gradual accumulation of limited amounts of secondary tissues produced annually. We acknowledge that size is a very imprecise measure of plant age and that this imprecision is compounded by the turnover of different species in a community as it occupies space. However, it is reasonable to postulate that maximum

plant size and community age are, on average, positively correlated such that the presence of old and large individuals denotes the relative absence of recent 'global' community disturbance.

The Gentry database does not provide information on plant age. However, analysis of the Cannell (1982) compendium shows that average stem diameter decreases dramatically with increasing plant density. More important, it reveals an inverse relationship between community age and density. This last relationship is weak ($r^2 = 0.222$, $n = 344$) but nevertheless significant statistically ($F = 114$, $P < 0.0001$). As average stem diameter is correlated with maximum stem diameter (and with the numerical values of α and β), we argue that there is sufficient evidence to accept the proposition that old, comparatively undisturbed communities have size frequency distributions with centroids skewed to the right, whereas the reverse is true for younger or recently disturbed communities (see Fig. 1c).

The relationships shown here for community size frequency distributions mirror those reported for population size frequency distributions. For example, Condit *et al.* (1998) show that static information on the size distribution of a population is not a good indicator of future population trends, but they also report that species with shrinking populations (decreasing plant density) have size frequency distributions with less negative regression slopes, whereas species with growing populations have more negative slopes, i.e. at the species level, population growth correlates negatively with the slopes of size distributions. In this regard, the average slope of the ordinary least squares regression curves for the Gentry community frequency distributions represented is -1.75 ($SE \pm 0.03$; minimum = -3.53 and maximum = -0.387); the average slope of the corresponding reduced major axis regression curves is -1.91 ($SE \pm 0.03$; minimum = -3.83 and maximum = -0.641). Regardless of the regression protocol used to establish the numerical value of α (i.e. Model Type I or II regression analysis), it is clear that significant variation exists among community size frequency distribution slopes that in turn correlates with community plant density.

This variation is important, especially in terms of estimates of total standing community stem biomass. Based on size frequency distributions with an average scaling exponent of -2 , Enquist & Niklas (2001) assert that total standing stem biomass is statistically 'invariant'. On average, this conclusion appears to be true. However, the numerical value of α varies significantly across the Gentry communities in a manner that we believe reflects the extent to which a particular community is dominated by larger and older individuals and thus comparatively undisturbed biologically or physically. As plant size and age

are crudely correlated, the effects of biological or physical disturbance cannot be neglected when evaluating community biomass relationships assessed on the basis of size frequency distributions.

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