Relationship between size hierarchy and density of trees in a tropical dry deciduous forest of western India

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Abstract

Questions: Density dependence is thought to restrict exponential growth as well as give rise to size structure in populations. Size hierarchy in trees from tropical dry deciduous forests is studied to ask (1) whether nature of competition is symmetric or asymmetric and (2) what is the self thinning trajectory under a natural gradient of tree density.

Location: Western India.

Methods: Density was measured as the number of trees in 10-m radius circular plots ($n = 96$) and size was measured at DBH. Size variation was evaluated by the Gini coefficient ($n = 1239$ trees).

Results: Size inequality between neighbours decreased with density but in a non-linear manner. In the backdrop of existing theory this indirectly suggests that competitive interactions may be symmetric over a 'depletive' resource such as below-ground water (rather than a 'pre-emptive' resource such as light), which is very plausible in a semi-arid environment. The self thinning coefficient derived from the relationship between stem diameter and density ($\gamma \approx -1/4$), is higher than expected from existing models of allometric plant growth ($\gamma \approx -1/3$) which are based on above-ground interactions alone. Seen in conjunction, these results suggest that above-ground structures, such as stem size, do not adequately represent the outcome of competitive interactions when below-ground resources, such as water, may be more important under semi-arid conditions.

Conclusions: The non-linear relationship between size inequality and density indicates that there exists a density threshold beyond which investment in above-ground biomass becomes sluggish in semi-arid, deciduous forests. Since current allometric models do not incorporate below-ground biomass for trees, these data suggest that a more comprehensive allometric growth model may have higher predictive power and wider applicability.

Keywords: Allometric growth; *Anogeissus pendula*; Below-ground competition; Density dependent growth; Limiting factor; Self thinning.

Nomenclature: Champion & Seth (1968).

Abbreviations: CI = Confidence interval; G = Gini coefficient.

Introduction

Density dependence is regarded as the major modifier of exponential population growth. Crowding reduces the growth rates of individuals but is dependent on the size of individuals (Vandermeer & Goldberg 2003). In plants, larger individuals can use a disproportionately large amount of resources leading to frequently observed size hierarchy in natural populations. Plant populations have numerous small individuals and a few large ones that comprise most of the population's biomass (Weiner 1985). The mechanisms determining size hierarchy in plants remain of keen interest since this has profound ecological and evolutionary significance as large individuals are capable of contributing inordinately to the gene pool of subsequent generations (Schwinning & Weiner 1998). Both theoretical and empirical work in this regard has focused on two aspects: (1) symmetric/asymmetric nature of plant competition where individuals may pre-empt a given resource depending on size and (2) self thinning with variation in density.

Whether or not size variation increases with crowding is related to the way resources are divided between competitors (Schwinning 1996). Theory suggests that size variation will increase with density if competition is size asymmetric, thus giving larger individuals an advantage over smaller ones at resource acquisition. Above-ground resources such as light are of such 'pre-emptable' nature (i.e. one-sided competition, Schwinning & Weiner 1998). Alternately; if competition is symmetric, size variation decreases with density and larger individuals do not have an advantage in acquiring 'depletive' resources such as water (i.e. two-sided competition, Schwinning & Weiner 1998). In this manner, plants are expected to respond to neighbourhood conditions in relation to their competitive ability over a limiting resource (Mack & Harper 1977). There has been much confusion on how best to measure size hierarchies in plant populations. Suggestions have ranged from skewness and variance of plant size (Turner & Rabinowitz 1983) to measures of inequality (Lorenz curves and Gini coefficients; Weiner & Solbrig 1984)

developed in economics (Sen 1973). The debate has been common surrounding the purported self thinning characteristics of plant populations.

There is general agreement that mass ($\bar{m}$) and density (N) are related by a simple power equation:

$$\bar{m} \propto N^{\gamma},$$ (1)

but it is uncertain whether the exponent is always γ = –3/2 as suggested by Yoda et al. (1963) (see also Reineke 1933). The debate is often seen as a conflict between isometric and allometric models (Weller 1987). Under isometry (Yoda et al. 1963), plants do not change shape during growth and γ is –3/2. However, under allometry (Mohler et al. 1978) growth is accompanied by change of shape and γ deviates from –3/2. Recently, plant-geometry has been incorporated in models relating size, growth and density (Enquist & Niklas 2001; Niklas et al. 2003a). New allometric models suggest that mean stem diameter ($\bar{D}$) is related to density as:

$$\bar{D} \propto N^{-1/2}$$ (2)

with the scaling exponent predicted between -0.48 and –0.55 (95% CI; Enquist & Niklas 2001). More detailed analysis (Gentry dataset) suggests that $N^{-1/3}$ with the scaling exponent between –0.37 and –0.29 (95% CI; Niklas et al. 2003b).

However, data that evaluate both these aspects – size asymmetry and self thinning – under natural conditions remain scarce. Here I present empirical data from a tropical, semi-arid, deciduous forest on variation in plant size (measured by stem diameter) with density to address: (1) whether plant competition in tropical deciduous forests is symmetric with regard to below-ground resources and (2) whether the patterns of self thinning observed in the tropical deciduous forests approach –1/3 (as expected under allometry).

Material and Methods

Study area

Data were collected between January and April 2001 in Ranthambhore National Park (392 km²), which is part of Ranthambhore Tiger Reserve (1334 km²; 26° N, 76° E), Rajasthan, western India. Vegetation of this region is tropical dry-deciduous, which extends across western and central India, covering an area approximately the size of England. *Anogeissus pendula*, *Acacia leucophloea* and *Butea monosperma* are the common trees forming the climax (Champion & Seth 1968). The forests are of relatively homog-

enous composition (87% of all trees are *A. pendula* (Champion & Seth 1968) but tree densities vary between ca. 150 and 900 trees/ha (Bagchi 2006). Since attaining protected area status in early 1970s these forests have not been harvested. I consider the existing natural density gradient to represent different points on the self-thinning trajectory as the forests recover from previous disturbances, in lieu of manipulating the density of trees. Reliable information about the extent and nature of past management practices are lacking but fuelwood extraction would have been a major form of disturbance four decades ago. In this regard, time is an associated independent variable in this study. Most authors agree that the role of history is important in assessing size distributions (Niklas et al. 2003b) as tree size and age are correlated (see later for further discussion). Other details of the study area can be found in Bagchi et al. (2003a, b; 2004) and Bagchi (2006) .

Data collection and analyses

Sampling plots (n = 99, 10-m radius circular plots 314 m² in size) were laid every 200 m on eight randomly laid transects in the study area (Bagchi et al. 2003a). Data on DBH (to the nearest cm) were collected from all trees > 6 cm DBH in these plots. Additionally, the total number of trees in a plot was noted as a measure of density; three plots did not have any trees and were removed from further analysis. These data were used to investigate the relationship between density and mean DBH. Size inequality was assessed using Lorenz curves and Gini coefficients (Weiner & Solbrig 1984). In the Lorenz curve, individuals were ranked according to their size and cumulative fraction of the population size was plotted against cumulative fraction of total population size. If individuals contribute to overall population size in proportion to their own size, then a straight line of equality is expected. However, competition results in disproportionate contributions from different size classes with a resultant deviation from the line of equality. This deviation was measured using the Gini coefficient (Sen 1973); defined as the one-half of the relative mean difference i.e. the mean of differences between all pairs of individuals:

$$G = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n^2 \bar{x}}$$ (3)

where x_i and x_j are the size of individuals i and j out of a total n and x is mean size. Following Dixon et al. (1987), 95% confidence intervals were obtained for G through re-sampling (1000 iterations). The G value was multiplied by n/(n–1) to obtain an unbiased value G' (Weiner 1985).

To check whether size inequality is related to density, G' was plotted against plant density with $n = 96$ plots. Analyses were carried out using spreadsheets and SAS v 9.0 (SAS Institute, Cary, NC, US).

Results

A total of 1239 trees from 11 species were recorded, with densities varying between one and 43 individuals per plot. *A. pendula* accounted for 87% of individuals and the three most common species represented > 95% of the total, making the data comparable to previous studies based on monocultures. DBH of trees was highly variable ranging from 6.4 cm to 84.2 cm (mean ± SD = 16.4 ± 9.7 cm). The size distribution in the population was biased towards intermediate sized individuals (Fig. 1). Very few individuals exceeded 30 cm DBH and 15-20 cm DBH appears to be the modal size class in these forests (Fig. 1, with 5-cm class intervals). Mean DBH decreased with density (Fig. 2). Plotting mean DBH against density on a $\log_{10}$ scale gave γ = –0.24 (–0.22 to –0.26, 95% *CI*) (Fig. 2).
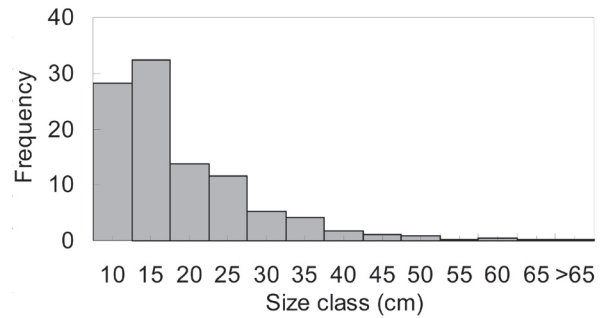

Fig. 1. Frequency distribution of size classes (5 cm class intervals of DBH) in trees of Ranthambhore Tiger Reserve, western India ($n = 1293$ trees from 96 plots).

This suggests that neighbours tend to grow to a similar size under crowding.

The Lorenz curves relating proportional contribution of size classes to overall population size show visible deviation from the hypothetical line of equality (Fig. 3). Gini coefficient for size inequality was $G' = 0.27$ (0.25 to 0.29, 95% *CI*). G' for the entire density gradient (ranging from one to 43 trees per plot, Fig. 4) declined
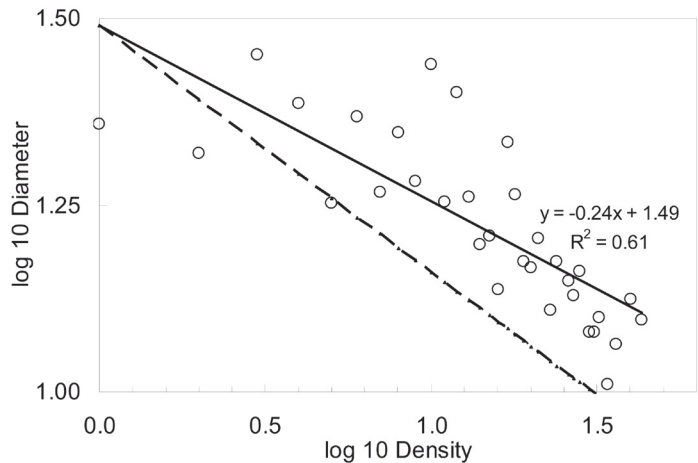
Fig. 2. Relationship between tree density (no. of trees per plot) and tree size (mean DBH in cm) to estimate self thinning in trees of Ranthambhore Tiger Reserve, western India ($n = 1293$ trees from 96 plots). The observed relationship (solid line) is seen to be significantly shallower than the -1/3 allometric self thinning line (broken line).
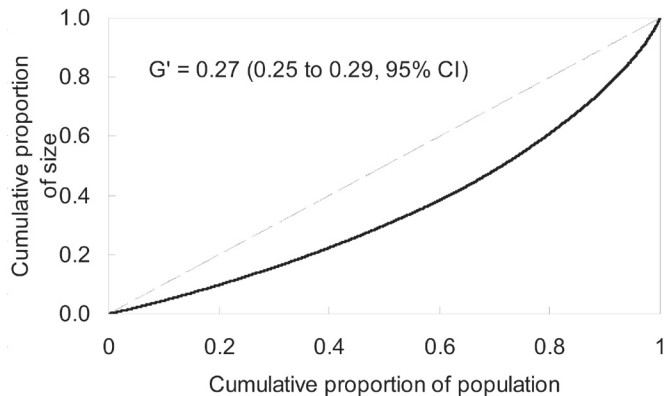

$y = -0.24x + 1.49$
$R^2 = 0.61$

Fig. 3. Lorenz curve representing size hierarchy in trees of Ranthambhore Tiger Reserve, western India, measured by the unbiased Gini coefficient (G'). ($n = 1293$ trees from 96 plots).
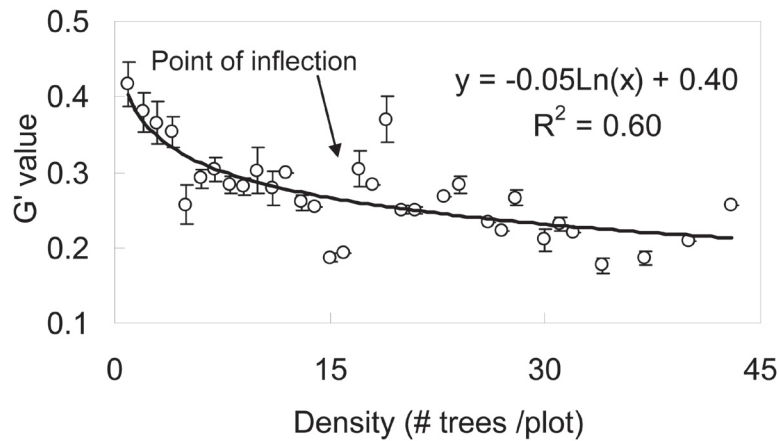

G' = 0.27 (0.25 to 0.29, 95% CI)

Fig. 4. Relationship between tree density (no. of trees per plot) and size-inequality in trees (measured by the unbiased Gini coefficient G'). Mean G' is calculated from DBH using 1000 bootstrap iterations (Dixon et al. 1987), with error bars showing ± 1 s.e. ($n = 1239$ trees from 96 plots). The observed non-linear relationship ($P < 0.01$, $R^2 = 0.60$) suggests that size inequality diminishes rapidly at low densities but tapers out beyond a threshold of ca. 16 trees per plot suggesting that above-ground structures are no longer important determinants of plant competition beyond this density threshold.

non-linearly with density showing a point of inflection close to 16 trees per plot. Change is more rapid initially than at higher densities. Up to this 'threshold' density (c. 16 trees per plot) the decline was very steep but, at higher densities, the change in G' was not as appreciable.

Discussion

These data demonstrate two important patterns – decreasing size variability with density and a high self thinning coefficient compared to predictions from existing allometry theory. Previous studies have determined self thinning coefficients of –1/2 (Enquist & Niklas 2001; Niklas et al. 2003a) and more extensive datasets suggest it is –1/3 (Gentry dataset, Niklas et al. 2003b). Since the observed coefficient is close to –1/3, there seems to be a close agreement with the general pattern described in Niklas et al. (2003b). However, closer inspection of the variation around the coefficients suggests a possible deviation in statistical terms (95% CI between –0.22 and –0.26 in this study; and between -0.37 and –0.29 from Niklas et al. 2003b). So, it remains arguable how closely do these data agree with the general trends across different biomes.

Conventionally, declining trend in size variability with density is interpreted as evidence for symmetric competition (Schwinning & Weiner 1998; Weiner et al. 2001; Stoll et al. 2002). While this is valid for data where density is the independent variable (as in studies where densities are experimentally manipulated). It is uncertain whether the same conclusion can be applied to these data as densities were not experimentally manipulated but time is an associated independent variable. Thus, strictly speaking, this result is indicative of, but not conclusive for, inferring symmetric plant competition as other potential explanations could include site specific differences

in the manner in which these forests are recovering from past disturbances. In addition, close scrutiny of Fig. 4 shows higher variation in G' at low density compared to high density. Since this suggests that both large and small individuals co-occur in the plots with fewer trees, one can not rule out asymmetric competition playing a role at low densities.

Since large scale experimental manipulation in such endangered ecosystems is not an option, we may rely on the other main result for inference. It is suggested that the non-linear relationship between size inequality and density can help explain why the observed self thinning coefficient is higher than that predicted by existing allometric models (even higher than –1/3 suggested by Niklas et al. 2003b).

Size inequality decreases with density but the pattern is non-linear. Between densities of one and 16 trees per plot, there is a rapid decline in size inequality but this tapers off at higher densities. This seems to suggest that above-ground plant structures no longer reflect the outcome of plant competition beyond a density threshold. Presumably, below-ground biomass becomes more important once trees have acquired a certain stem size. Indeed, the modal size class in these forests seems to be 15-20 cm DBH as most individuals are of this size. Hence, after trees have grown to this size, they may invest in roots rather than in above-ground structures under the semi-arid and drought prone conditions. Influenced by the monsoonal climate, these forests endure semi-arid conditions, receiving only ca. 800 mm of rainfall annually with frequent drought years (Bagchi et al. 2003a, b). Thus, water (a below-ground resource) is likely to be the primary contested resource in such deciduous forests, instead of light as the trees are leafless for six months of the year. The decline of size inequality with density corroborates this possibility. Invoking the ideas of Stoll et al. (2002) and Stoll & Weiner (2000), the results seem

to indicate that local competitive interactions result in all neighbours being similar in size and that there is a lack of selective advantage to grow bigger than 15-20 cm DBH (i.e. the observed modal size Fig. 1). If water is the primary contested resource, then investment in roots would be vital rather than above-ground structures beyond a density threshold (which appears to be 16 trees per plot in the study area). Many authors agree that ignoring the potential influence of below-ground plant biomass in determining the outcome of density dependent interactions is a drawback of current allometric growth models (Enquist & Niklas 2001; Niklas et al. 2003a). Data presented here seem to highlight the relevance of density dependence on below-ground interactions (Gersani et al. 2001). Evolving methods to incorporate below-ground structures into existing theory promises to be a challenging prospect for future research.

Allometric growth in plants has interested biologists for a long time and several theories have been proposed to explain patterns observed in natural and experimental populations. Yet, given the general lack of understanding of the main mechanisms causing such patterns, there is little agreement between these models. In conclusion, the data presented here lead to certain noteworthy generalizations: (1) in monsoonal dry-deciduous forests competition between trees is likely to be size symmetric at higher densities because below-ground resources (such as water) are the limiting factors and below-ground plant biomass may precede stem size in importance, (2) this possibility gives rise to testable hypotheses such as increased investment in root biomass at high densities rather than in stems. This, in turn, may yield a higher than expected self thinning coefficient.

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