Plant height–crown radius and canopy coverage–density relationships determine above-ground biomass–density relationship in stressful environments

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Debate continues in theoretical ecology over whether and why the scaling exponent of biomass–density (M – N) relationship varies along environmental gradients. By developing a novel geometric model with assumptions of allometric growth at the individual level and open canopy at the stand level, we propose that plant height–crown radius and canopy coverage–density relationships determine the above-ground M – N relationship in stressful environments. Results from field investigation along an aridity gradient (from eastern to western China) confirmed our model prediction and showed that the above-ground M – N scaling exponent increased with drought stress. Therefore, the ‘universal’ scaling exponents ($-3/2$ or $-4/3$) of the M – N relationship predicted by previous models may not hold for above-ground parts in stressful environments.

Keywords: abiotic stress; allometric growth; aridity gradient; geometric model; self-thinning

1. INTRODUCTION

Because both the $-3/2$ and $-4/3$ exponents of biomass–density (M – N) relationship have been criticized on theoretical and empirical grounds (e.g. Enquist *et al.* 1998; Kozłowski & Konarzewski 2004; Deng *et al.* 2006), controversy continues over the underlying value and variability of the M – N scaling exponent. Some recent literature indicates that the above-ground M – N scaling exponent (α) varies with environmental conditions such as soil fertility (Morris 2003) and water availability (Deng *et al.* 2006).

There are two basic assumptions underlying the ‘universal exponent’ theories (e.g. $-3/2$ and $-4/3$ exponents): isometric growth at the individual level and closed canopy at the stand level (Yoda *et al.*

1963; Enquist *et al.* 1998). However, neither of them may hold in environments characterized by abiotic stress (i.e. resource limitation). First, allometric growth leads to a generally optimal allocation pattern over the course of growth and development, thus maximizing the uptake of limiting resources (Weiner 2004). Previous studies have shown that the plant height–crown radius (H – r) relationship is allometric rather than isometric (Peper *et al.* 2001; Osunkoya *et al.* 2007), and its scaling exponent can be influenced by soil fertility (Morris & Myerscough 1991; Morris 1999). Our field investigation also showed that the H – r relationship changed from isometric in benign environments (high soil water availability, no neighbours) to allometric at arid sites (X. Jia 2008, unpublished data). Second, open canopy is common for vegetation in stressful environments (e.g. arid and infertile areas), even when plant biomass is at carrying capacity for the given density (on or close to the self-thinning line) (Fowler 1986; Deng *et al.* 2006). Therefore, we propose that allometric growth and open canopy in stressful environments may result in the deviation of α from universal values ($-3/2$ or $-4/3$).

To test this hypothesis, we (i) developed a geometric model to illustrate how allometric growth and open canopy can influence α and (ii) examined the model assumptions and predictions by a field investigation along an aridity gradient from eastern to western China.

2. MATERIAL AND METHODS

(a) Model

The model is based on an assumption that biomass density is constant across species and sites (Yoda *et al.* 1963). Accordingly, plant above-ground biomass (M) is proportional to its canopy volume:

$$M \propto r^2 H, \quad (2.1)$$

where r is the crown radius and H is the shoot height. There is mounting evidence that an allometric relationship exists between H and r (e.g. Osunkoya *et al.* 2007), thus:

$$H \propto r^\beta. \quad (2.2)$$

If plant canopies do not overlap, r can be expressed as a function of canopy coverage (C) and plant density (N):

$$r \propto \left(\frac{C}{N}\right)^{1/2}. \quad (2.3)$$

Incorporating expressions (2.2) and (2.3) into expression (2.1) yields:

$$M \propto \left(\frac{C}{N}\right)^{(2+\beta)/2}. \quad (2.4)$$

We presume an allometric relationship between C and N , as:

$$C \propto N^\delta. \quad (2.5)$$

If canopy coverage is constant over the course of self-thinning (for example, $C = 100\%$ in benign environments), δ should be 0. In contrast, if survivors do not (completely) grow into the canopy space vacated by the death of suppressed plants, δ should be positive. The latter case has been observed in environments with very low soil fertility and was explained by the increased contribution of below-ground competition to the thinning process (Morris 1999). We expect that the C – N relationship may also exist in other stressful environments where canopies are open (e.g. arid areas). Incorporating expression (2.5) into (2.4) gives the M – N relationship as:

$$M \propto N^{(2+\beta)(\delta-1)/2} \quad (2.6)$$

or

$$\alpha = (2 + \beta) \frac{\delta - 1}{2}. \quad (2.7)$$

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Table 1. The main geographical and climatic conditions of the three experimental sites. Aridity index = $\log (E/P)$, where E is the annual mean potential evaporation and P is the annual mean precipitation.

parameters	sites		
	Tianmu	Dengfeng	Guazhou
latitude	30°20' N	34°30' N	40°40' N
longitude	119°26' E	112°55' E	95°41' E
altitude (m)	381	616	1250
annual mean temperature (°C)	14.8	10.2	8.8
annual mean precipitation (mm)	1390	563	45.7
annual mean potential evaporation (mm)	1249	1300	3140.6
aridity index	−0.046	0.36	1.83

An assumption underlying expressions (2.6) and (2.7) is that plant biomass is at carrying capacity for the given density (on or close to the self-thinning line) (Deng et al. 2006).

(b) **Field investigation**

In the summer of 2008, we collected field data from plant communities at three sites along a natural aridity gradient from eastern to western China (table 1). Within each site, square quadrats of different sizes were established according to vegetation types (i.e. tree, shrub or herbaceous quadrats). We measured the diameter at breast height (*DBH*) of trees, the height (H) and crown radius of trees and shrubs (crowns were viewed as ellipses in a two-dimensional space, the geometric mean of long and short radii was used as an estimation of r) and the above-ground biomass (fresh weight) of shrubs and herbs in each quadrat. Subsamples of above-ground materials were taken for each shrub and herbaceous species. These materials were used to measure dry/wet mass ratio and calculate dry biomass for each species. Above-ground biomass of trees was estimated by H and *DBH* according to empirical equations (Lu & Batistella 2005). Mean above-ground biomass (M) was calculated, and plant density was recorded for each quadrat. Canopy coverage was calculated as the ratio of total canopy area to quadrat size.

The scaling exponents and intercepts of H – r , C – N and M – N relationships were estimated by the reduced major axis (RMA) regression of log-transformed data. If a predicted α (derived from equation (2.7)) was embraced in the 95 per cent confidence interval of its observed value (derived from $\log M$ – $\log N$ regression), the difference was considered to be non-significant. We combined our data with those from Deng et al. (2006) to examine the relationship between α and the aridity index. Akaike information criterion (AIC) was used to select the best regression model from linear, quadratic and cubic functions (Burham & Anderson 1998) (see appendix S1 in the electronic supplementary material for more detailed information about field investigation).

3. RESULTS

The H – r scaling exponent (β) decreased with increasing drought stress (aridity index), while the C – N scaling exponent (δ) showed an inverse trend (table 2; figures S1 and S2 in the electronic supplementary material). Most importantly, the predicted α for the three sites was statistically indistinguishable from their observed values (table 3; figure S3 in the electronic supplementary material).

Furthermore, α increased with drought stress as being best described by a quadratic function (figure 1; AIC for linear, quadratic and cubic models

Figure 1. Scaling exponent (α) of the above-ground biomass–density relationship increases with aridity index. The α values from both our results and Deng et al. (2006) are shown. Bars indicate 1 s.e. Filled circles, our data; open circles, Deng et al. (2006). $y = -1.59 + 0.63x - 0.17x^2$ ($R^2 = 0.95$, $p = 0.01$).

are -24.51 , -29.11 and -27.99 , respectively). Interestingly, the $-3/2$ or $-4/3$ exponent only held when drought stress was low (i.e. in benign environments).

4. DISCUSSION

Results from the field investigation confirmed our model prediction that H – r and C – N relationships (i.e. β and δ) determine the above-ground M – N relationship (i.e. α) in stressful environments (equation (2.7); table 3). Furthermore, α was not invariant, but increased with drought stress (figure 1). Flatter above-ground M – N relationships have also been observed in environments with low light (Lonsdale & Watkinson 1982) or nutrient (Morris 2003) availability.

Plant allometric growth is usually an adaptive trait to maximize the uptake of limiting resources and to promote whole-plant growth in environments characterized by abiotic stress (i.e. resource limitation). In fact, plants ‘evolve towards the optimal allometric trajectory’ and adjust the trajectory adaptively (plasticity) (Weiner 2004). Our results showed that β decreased with increasing drought stress (table 2; figure S1 in the electronic supplementary material). This is consistent with the case in low-nutrient environments (Morris 1999). In benign environments where plants compete primarily for light, rapid height growth is crucial for effective light interception (King 1990). Therefore, plants in such environments should have higher β (i.e. as plants grow larger, they tend to have greater height growth for a given amount of radial extension). Whereas in arid environments, light competition is usually less important relative to below-ground competition for water (Deng et al. 2006). In addition, the energy cost of vertical water transport (Koch et al. 2004) may arise when water availability is low. Therefore, plants in arid environments should have smaller β (i.e. as plants grow larger, they tend to have less height growth for a given amount of radial extension).

Open canopy is a common feature in stressful environments such as arid or infertile areas, even

Table 2. Scaling exponents and intercepts (IT) of H – r and C – N relationships (see expressions (2.2) and (2.5)) at three sites, as estimated by the RMA regression of log-transformed data. * $p < 0.05$, ** $p < 0.01$.

sites	H – r relationship				C – N relationship			
	β (s.e.)	IT (s.e.)	n	R^2	δ (s.e.)	IT (s.e.)	n	R^2
Tianmu	1.34 (0.06)	0.32 (0.03)	269	0.49**	0.02 (0.001)	1.95 (0.002)	25	0.80**
Dengfeng	0.86 (0.03)	0.68 (0.01)	517	0.24**	0.02 (0.002)	1.94 (0.003)	27	0.53**
Guazhou	0.64 (0.02)	–0.36 (0.01)	205	0.79**	0.32 (0.06)	1.06 (0.04)	30	0.15*

Table 3. Scaling exponents (α) and intercepts (IT) of the above-ground M – N relationship at three sites, as estimated by the RMA regression of log-transformed data. Predicted α was calculated according to equation (2.7). * $p < 0.01$.

sites	α (s.e.)	95% CI of α	IT (s.e.)	n	R^2	α (predicted)
Tianmu	–1.65 (0.03)	–1.72, –1.58	0.97 (0.06)	25	0.99*	–1.65
Dengfeng	–1.30 (0.06)	–1.43, –1.18	0.48 (0.08)	27	0.95*	–1.41
Guazhou	–1.01 (0.10)	–1.20, –0.81	–1.16 (0.08)	30	0.74*	–0.90

when plant biomass is at carrying capacity for the given density (on or close to the self-thinning line) (Deng *et al.* 2006). Our results showed that canopy coverage decreased with density (positive δ) at the most arid site (table 2; figure S2 in the electronic supplementary material). This can occur over the course of self-thinning when survivors do not (completely) grow into the canopy space vacated by the death of suppressed plants. Morris (1999) also found that shoot growth (thus canopy area) of *Ocimum basilicum* plants was static over the course of self-thinning in environments with very low fertility. Open canopy, positive δ and decreased β (thus increased α) collectively indicate that self-thinning in arid or infertile environments may be driven by below-ground interactions, i.e. above-ground allometries here were following self-thinning, rather than driving it (Morris 2003).

With respect to the above-ground M – N relationship, neither the $-3/2$ nor $-4/3$ exponent held across the entire aridity gradient (figure 1). Since previous data supporting a universal exponent were largely derived from relatively benign environments with closed canopies (e.g. Enquist *et al.* 1998), a value of α around $-3/2$ or $-4/3$ was more likely to be detected. Although our model was only tested across an aridity gradient and needs further verification, we propose that a universal exponent of the above-ground M – N relationship may not hold in stressful environments.

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