

# Plant mass–density relationship along a moisture gradient in north-west China

JIAN-MING DENG\*, GEN-XUAN WANG\*†, E. CHARLES MORRIS‡  
XIAO-PING WEI\*, DONG-XIU LI\*, BAO-MING CHEN§,  
CHANG-MING ZHAO\*, JING LIU\* and YUN WANG\*

\*Key Laboratory of Arid and Grassland Agroecology at Lanzhou University, Ministry of Education, Lanzhou 730000, China, †College of Life Sciences, Zhejiang University, Hangzhou 310029, China, ‡Ecology and Environment Research Group, Hawkesbury Campus (K12), University of Western Sydney, Locked Bag 1797, South Penrith DC, Australia 1797, and §State Key Laboratory of Biocontrol, School of Life Science, Sun Yat-Sen (Zhong Shan) University, Guangzhou 510275, China

## Summary

**1** Metabolic scaling theory predicts that the rate of resource use per unit area is independent of the average mass per individual and that the slope of the log mass–log density relationship should be  $-4/3$ .

**2** Data were obtained from plant communities along a natural gradient of moisture and latitude in north-west China to test the generality of this theory.

**3** The allometric exponents (slopes of the log mass–log density relationship) for above-ground biomass decreased with natural moisture levels and plant cover, deviating from the predictions of the energy equivalence theory. Allometric exponents for below-ground and total biomass were similar among the three sites and were much closer to the predicted value of  $-4/3$ .

**4** Metabolic scaling theory may be applicable under many growth conditions, but not when restricted to above-ground biomass under drought stress. The rate of supply of the limiting resource per unit area determines which plant parts behave according to theory.

*Key-words:* above- and below-ground biomass, allometric exponents, aridity index, competition, energy equivalence, maximum density

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## Introduction

Based on a model of fractal structure, West *et al.* (1997, 1999a) argued that the metabolic rate (or use rate of resources) per individual would scale with  $M^{3/4}$ . If resource supply rate ( $R$ ) per unit area is held constant, then maximum population density should vary inversely with body size  $M^{-3/4}$  (Enquist *et al.* 1998; Brown *et al.* 2004). There has been support for this prediction from a variety of plant communities (Enquist *et al.* 1998; Enquist & Niklas 2001; Enquist *et al.* 2003; Brown *et al.* 2004). Enquist *et al.* (1998) presented data from 37 plant species showing that the rate of resource use ( $Q$ ) by individual plants scales approximately as the  $3/4$  power of plant mass ( $M$ ):  $Q \propto M^{3/4}$ . In addition, their re-analysis of data from 251 populations showed that the scaling relationship between maximum plant

population density ( $N_{\max}$ ) and plant mass also obeys  $3/4$ -power scaling, with  $N_{\max} \propto M^{-3/4}$ . Therefore, given the correlation between  $Q$  and  $N_{\max}$ , we may deduce that the rate of resource use per unit area ( $N_{\max} \cdot Q$ ) will be independent of the average mass per plant (Enquist *et al.* 1998):  $N_{\max} \cdot Q$  is proportional to  $M^{3/4} \cdot M^{-3/4}$ , i.e. to  $M^0$ . The regression slopes of the mass–density relationship in early post-fire chaparral succession obey the ‘ $-4/3$  power rule’ (i.e.  $M \propto N_{\max}^{-4/3}$ , Guo & Rundel 1998). The energy equivalence relationship is controversial, however, and requires further testing (Damuth 1998; Dewar 1999; Magnani 1999; Dodds *et al.* 2001). Kozłowski & Konarzewski (2004) have argued that the  $3/4$  scaling of metabolic rate derived from the model is mathematically incorrect and based on assumptions that are biologically unjustified.

Predictions of the metabolic theory have been tested with data on above-ground biomass, usually without drought stress (Enquist *et al.* 1998, 2003; Dewar 1999; Bi *et al.* 2000; Enquist & Niklas 2001; Bi 2004). Energy

equivalence assumes that (i) once plant canopies have reached closure, most of the incident radiation per unit area is intercepted (Newton & Blackman 1970; Dewar 1999), and (ii) for well-watered plants, growth rate per unit of intercepted radiation (that is, the light utilization efficiency, or LUE) is nearly independent of plant above-ground biomass (Dewar 1999). Plant stands experiencing severe drought conditions often show an open canopy and increased root:shoot ratio (Zhang *et al.* 1995). It is therefore reasonable to ask whether above-ground biomass fits the proposed allometric model under such conditions. Let us assume that (i) there is drought stress and the density of individual plants per unit area is at its maximum ( $N_{\max}$ ), (ii) the root mat is dense enough to take up all the available below-ground water, (iii) growth rate per unit of water resource taken up is therefore independent of plant below-ground biomass, and (iv) the mean rate of resource use ( $Q$ ) scales as  $M^{3/4}$  (Enquist *et al.* 1998; Enquist & Niklas 2001; Brown *et al.* 2004; see also West *et al.* 1997, 1999a, 1999b). If  $N_{\max} Q \propto M^r$  holds for below-ground parts under drought conditions, below-ground biomass varies with density, as  $M \propto N^{-4/3}$ . But if plant mass–density relationships are driven by below-ground interactions, the allometric exponents for above-ground biomass may decrease under drought conditions, so that  $M \propto N^{-r}$  (where  $r$  is less than  $4/3$ ). In such cases, the rate of resource supply ( $R$ ) per unit area for above-ground biomass is expressed by  $R = N_{\max} \bar{Q} \propto M^{-1/r} M^{3/4} = M^{-1/r+3/4} = M^a$ , where  $\bar{Q}$  is the average rate of resource use per individual, and  $a$  will be negative.

In the arid and semi-arid central part of Gansu province, China, there is a natural precipitation gradient associated with latitude (Pan *et al.* 2003). This

situation provides an ideal opportunity to test the  $M$ – $N$  relationship in plant communities under drought stress.

Methods

The experiments were conducted in natural communities at three sites (Lanzhou, Baiyin and Jingtai) in the central part of Gansu province, China, which are classified as arid or semi-arid. The climatic conditions of the sites are similar except for rainfall, which decreases as latitude increases, and evaporation, which increases with latitude (Table 1). The soil properties of the three sites are similar (Pan *et al.* 2003), i.e. orthic entisols of yellow earth in Loess Plateau (Gong 1999). The vegetation is composed mainly of shrub-dominated communities, and the species diversity is relatively low. Important community characteristics, including the sizes of individual plants, plant cover and species diversity, vary greatly along the moisture/latitudinal gradient and only Lanzhou has a closed canopy (Table 2). Most plants are xerophytes.

Data were collected in July 2003 for up to 32 species at each of the three sites. As plant density and size showed variation over nearly 5 and 8 orders of magnitude, respectively, within sites, square quadrats were established with sides of either 40 cm, 1 m, 2 m, 3 m, 10 m or 20 m. Stands with different densities were sought and three quadrats of an appropriate size were placed randomly for each density level at each site. The number of species, the number of individuals, canopy cover, above-ground biomass and below-ground biomass of each species were measured in each quadrat. Plants were harvested and fresh above-ground and below-

**Table 1** The main geographical and climatic conditions of the three experimental sites in China. Aridity index =  $\log_{10}(E/P)$ , where  $E$  is annual mean potential evaporation,  $P$  is annual mean precipitation

Parameters	Sites		
	Lanzhou	Baiyin	Jingtai
Latitude	35°48'–35°58' N	36°43'–36°49' N	37°18'–37°26' N
Longitude	103°53' E	104°11' E	104°03' E
Altitude (m)	1575	1707	1631
Annual mean temperature (°C)	9.1	8.0	8.2
Annual mean precipitation (mm)	346	209	192
Annual mean potential evaporation (mm)	1342	1852	2673
Aridity index	0.59	0.95	1.14

**Table 2** Characteristics of natural vegetation of the three experimental sites in China. Mean  $\pm$  1 SD

Parameters	Sites		
	Lanzhou	Baiyin	Jingtai
Total number of species investigated	32	16	11
Number of quadrats	174	153	117
Size range of quadrats (m <sup>2</sup> )	0.16–100	0.16–400	0.16–400
Mean vegetation cover (%)	96 $\pm$ 3.24	63 $\pm$ 5.04	37 $\pm$ 4.47
Mean root:shoot ratio	0.92 $\pm$ 0.31	1.92 $\pm$ 1.42	2.18 $\pm$ 1.61

ground biomass was determined. The below-ground biomass was harvested by the soil monolith method of Hauser (2000): although fine roots were filtered out with a 0.5-mm mesh sieve, there is still an inevitable loss during sampling. Sub-samples of above-ground and below-ground material were taken for each species, and weighed after oven-drying at 65 °C for 72 hours, and the dry/wet mass ratio was used to calculate the total dry biomass for each species.

Because below-ground competition is thought to be the dominant plant–plant interaction in arid and semi-arid regions (Fowler 1986; Zhang *et al.* 1995), and above- and below-ground competitions can interact (Donald 1958; Wilson 1988; Cahill 1999), we plotted each of mean above-ground biomass, below-ground biomass and total individual biomass against population density, at each site. The allometric exponents or slopes ( $-r$ ) and the intercept were estimated by the reduced major axis (RMA) regression of log-transformed data. Mean cover and the annual mean aridity index at the three sites were used as independent variables in multiple linear regression models using SPSS, with above-ground parts and below-ground parts, respectively, as dependent variables.

Results

The allometric exponents for the above-ground biomass vs. density relationship decreased from the Lanzhou site to the Jingtai site (Table 3, Fig. 1). This decrease in the slope of the log biomass – log density relationship above ground corresponded with decreasing trends in both annual mean precipitation and mean vegetation cover (Table 2). Only at Lanzhou, where vegetation cover was nearly complete, was the slope close to  $-4/3$ : Baiyin and Jingtai had much lower cover (Table 2) and the regression slopes were much shallower (Table 3, Fig. 1).

For below-ground and total biomass, the mass-density exponent showed little variation across the rainfall gradient, while the regression slopes for below-ground biomass-density at Baiyin and Jingtai were significantly steeper than those of above-ground

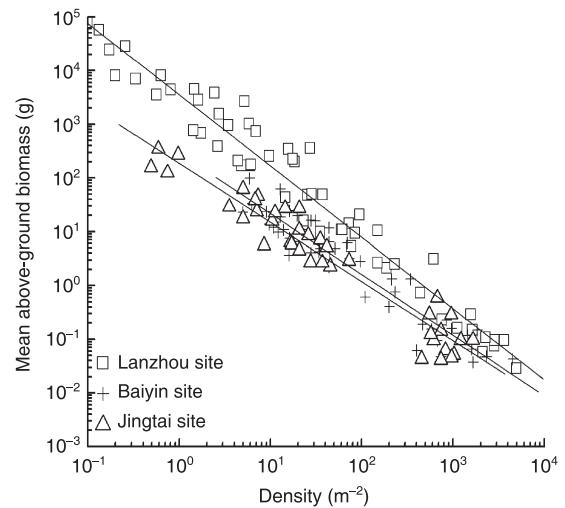


Fig. 1  $M$ – $N$  relationships between above-ground biomass and plant density at three sites along a natural moisture gradient in Gansu, China. All regressions were significant at  $P < 0.0001$  and the 95% CI of the slopes indicated that the exponents were statistically different from  $-4/3$ , except for the Lanzhou site.

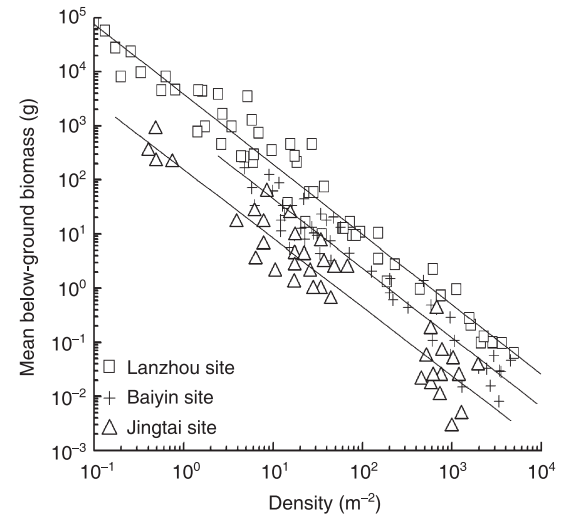


Fig. 2  $M$ – $N$  relationships between below-ground biomass and plant density at the three sites. All regressions were significant at  $P < 0.0001$ ; none of the exponents were statistically different from  $-4/3$ .

Table 3 Slopes and intercepts of linear relationship between the mean above-ground, below-ground and total biomass and the density at three sites, as estimated by reduced major axis. SE is standard error; IT is intercept

Sites	Regression $M: D$	Slope	SE	IT	SE	$R^2$
Lanzhou	Above ground	–1.34	0.03	3.58	0.07	0.96
	Below ground	–1.34	0.03	3.63	0.07	0.95
	Total	–1.33	0.03	3.90	0.07	0.96
Baiyin	Above ground	–1.14	0.06	2.57	0.11	0.91
	Below ground	–1.33	0.06	3.23	0.12	0.91
	Total	–1.28	0.05	2.97	0.12	0.88
Jingtai	Above ground	–1.11	0.06	2.47	0.12	0.91
	Below ground	–1.32	0.08	2.47	0.15	0.89
	Total	–1.27	0.06	2.29	0.11	0.98

parts (Table 3, Figs 1 and 2). Mean below-ground allocation increased with total biomass, indicating that the root:shoot ratio of plants is higher in drier environments (Table 2).

Assuming that the rate of resource use and metabolic rate scale as  $M^{3/4}$ , the relationship between the rate of resource supply ( $R$ ) and the average above-biomass of plants ( $M$ ) was estimated by the ‘energy equivalence model’ of Enquist *et al.* (1998). For above-ground biomass at the two drier sites, the exponent,  $a$ , in this relationship depended on the power exponent ( $r$ ) of the relationship between mean biomass per individual and density (i.e.  $R \propto M^a$ , where  $a = -1/r + 3/4$ , see Methods).

Thus the absolute value of the power exponent ( $a$ ) in Baiyin and Jingtai increased sharply compared with its value at Lanzhou, where  $a \approx 0$ , making it the only site where the value is consistent with the predictions from Enquist's model (Table 3; Enquist *et al.* 1998).

The 95% confidence interval of  $a$  for above-ground, below-ground part and total biomass were estimated at the three sites, substituting either the upper or lower value of the 95% confidence limits of  $r$  into the equation  $a = -1/r + 3/4$ . The confidence intervals were  $-0.016$  to  $0.039$ ,  $-0.035$  to  $-0.162$  and  $-0.060$  to  $-0.252$  for above-ground biomass in Lanzhou, Baiyin and Jingtai. Corresponding values for below-ground biomass were  $-0.318$  to  $0.022$ ,  $-0.064$  to  $0.039$  and  $-0.059$  to  $0.093$ , and  $-0.043$  to  $0.037$ ,  $-0.089$  to  $0.007$ , and  $-0.088$  to  $0.010$  for total biomass. Except for above-ground biomass at the two drier sites, the 95% confidence limits for  $a$  include zero.

In addition to changes in the absolute value of the allometric exponents for the above-ground biomass–density relationship, species diversity and total cover also decreased with the decline in annual mean precipitation (Table 2) as did LAI (data not shown).

## Discussion

It is well known that many characteristics of vegetation change under drought stress (Parker & Martin 1952; Negbi & Evannari 1961; Robberecht *et al.* 1983). The slopes of  $M$ – $N$  regression lines for the above-ground parts of plants become significantly shallower when water is severely limiting (Table 3; Fig. 1), similar to results observed under low light (Westoby 1977; Lonsdale & Watkinson 1982; Dunn & Sharitz 1990) or nutrient levels (Morris & Myerscough 1985, 1991, 1996).

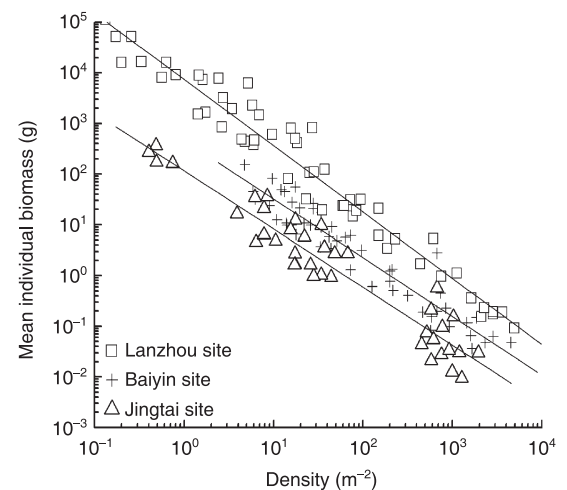
While some researchers have claimed that competition does not occur at all in deserts (Shreve 1942; Went 1955) or that the competition is less important in such 'high stress' habitats (Grime 1977), recent results show that competition among plants is both common and readily detected in deserts and in dry grassland (Fowler 1986). Plants compete primarily for limited water resources in drought environments (Wright 1970; King & Woodell 1973; Fowler 1986), which causes an increase of the root:shoot ratio, and decrease in cover, plant size and density (Table 2).

Although the plant canopy is not closed in the two drier sites, we assume that plant biomass may be at the carrying capacity of the environment (Fowler 1986). Under limited resources, such as those found in arid and semi-arid regions, plant stands may maintain a relatively steady structure and energy balance during the thinning process. Log  $M$ –log  $N$  regression lines may therefore reflect the self-thinning process. While the relationship between the  $-4/3$  scaling relationship and self-thinning is beyond the scope of this paper, we conclude that any plant thinning rule based on above-ground parts alone may not be appropriate for dry environments.

Positive interactions among plants are most common in habitats with high degrees of abiotic stress (Schenk *et al.* 2003), and facilitation has been long noticed in deserts (Shreve 1931, 1942; Fowler 1986). Our results suggested that the allometric  $M$ – $N$  exponents were lower for above-ground parts as drought stress increased, suggesting that the allometric exponents (or regression slopes) might even become positive under the most extreme conditions where facilitation is commonly observed. In that case, the size of an individual would increase with density because of the positive effect of the neighbouring plants.

Unlike above-ground biomass, below-ground parts do not show a marked decrease in the  $M$ – $N$  regression slope with decreases in the natural moisture level and cover. At the Lanzhou site, the regression slope for the above-ground parts ( $-1.335$ ) was much closer to the  $-4/3$  rule (West *et al.* 1997; Damuth 1998; Enquist *et al.* 1998), and was significantly steeper than that in Baiyin ( $-1.139$ ) and Jingtai ( $-1.108$ ). Regression slopes for the below-ground parts were close to  $-4/3$  at all sites (Table 3, Figs 2 and 3). This suggests that, under drought conditions, below-ground biomass, and perhaps total biomass, may show the predicted behaviour.

According to the general model of energy equivalence,  $R = N_{\max} \bar{Q}$ ,  $R$  is constant, at equilibrium in any given environment (Enquist *et al.* 1998). In other words, as long as plants grow until they are limited by resources (Tilman 1988; Chapin 1993; Huston & DeAngelis 1994; Enquist *et al.* 1998), the rate of resource supply or productivity per unit area will not vary with body size. As plants exchange resources or energy between the external and internal environments through their total leaf area,  $a$ , it may be assumed that the relationship  $R \propto a$  (West *et al.* 1999a) should be applicable to all plant types under all conditions. However, the model is not supported by our data under severe



**Fig. 3**  $M$ – $N$  relationships between the whole individual biomass and plant density at the three sites. All regressions were significant at  $P < 0.0001$ ; none of the exponents were statistically different from  $-4/3$ .

drought stress (Table 3, Fig. 1) or by the data of Wei *et al.* (2005) showing that slope of the  $M$ – $N$  regression for above-ground material is positively related to mean cover and negatively related to aridity index, while below-ground material shows small positive responses to both. This finding seems to be consistent with that of Dewar (1999), who argued that the rate of resource use by plants per unit area ( $R$ ) for growth may not be independent of plant mass under water-limited conditions. Interestingly, however, values of the power exponents ( $a$ ) for the below-ground part and the whole individual were much closer to the predicted values than those for above-ground biomass, suggesting that, under strong drought stress, metabolic theory is only applicable to below-ground or total biomass.

Although both Enquist's model and our studies propose that there are limited resources, the critical factors differ (spatially limited resources or light in Enquist *et al.* (1998); water and, possibly, nutrients in our studies). According to Leibig's law of the limiting factor, the population density should be determined by water resources rather than light or space under severe drought. According to the optimization theory (Donald 1968; Richards 1991; Zhang *et al.* 1999; Pan *et al.* 2003), root/shoot ratios are determined by the limiting resource. In short, the supply rate of the limiting resource per unit area determines which plant parts behave according to theory.

The power exponent ( $a$ ) for below-ground biomass or whole individual biomass still deviates from the theoretical value under drought stress, but the difference is not significant. Therefore, we may not yet reject the hypothesis of  $a = 0$  for all sites.

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