

Biomass-density relationship varies with water use efficiency across an aridity gradient

NAN WANG^a, JING GAO^a, SHAN-SHAN XU, WEI-PING ZHANG, GEN-XUAN WANG*

College of Life Sciences, Zhejiang University
CN-310058 Hangzhou, PR China
E-mail: fzstsys2@zju.edu.cn

ABSTRACT

Accumulating evidence has shown that the scaling exponent (α) of the aboveground biomass-density relationship is not a constant value. Debate continues over what determines the variation in α . By measuring foliar stable carbon isotope, plant morphological traits and α along an aridity gradient from eastern to Western China, we confirmed that the variation in α was accounted for by changes in plant morphological traits which are adaptive strategies for enhancing water use efficiency during drought stress. This information can be crucial for understanding and predicting community and ecosystem processes.

Keywords: scaling exponent, plant morphological traits, foliar stable carbon isotope.

Simple Euclidean geometry predicts a $-3/2$ power law of the relationship between mean aboveground individual biomass and density [1], while based on a model of fractal-like networks of branching tubes the exponent of biomass-density scaling should be $-4/3$ rather than $-3/2$ [2]. Although both exponents have been widely used by ecologists, and each has been supported by empirical studies, controversy continues in both theoretical and empirical areas of research over whether there is a universal exponent [3–6]. Accumulating evidence has shown that the scaling exponent (α) of biomass – density relationship is not a constant, but rather changes across environmental gradients [7–9]. A consistent scaling law becomes gradually fainter [10].

The population-level processes are considered as the manifestation of individual plant traits and plant-plant interactions [11]. Previous works illustrated that the effects of abio-

tic factors on population and community dynamics can be indirectly attributed to changes in individual [8; 12–15]. Although isometric growth at the individual level and closed canopy at the stand level are two basic assumptions underlying the scaling law (e.g. $-3/2$ and $-4/3$ exponents), Dai et al. (2009) developed a geometric model [$\alpha = (2 + \beta)(\delta - 1)/2$; β is the scaling exponent of shoot height (H) – crown radius (r) relationship, δ is the scaling exponent of canopy coverage (C) – plant density (N) relationship] to illustrate how allometric growth and open canopy under drought stress can influence α . Dai et al. (2009) also showed that increases in δ and declines in β could cause increases in α . So far few studies have explored what mechanism drives variations in α due to changes in δ and β , although this information can be crucial for understanding and predicting community and ecosystem processes.

Some variations in individual traits are adaptive strategies for living under different environmental conditions. Water is the most limit-

^aThese authors contributed equally to the study.

ing resource for plant in arid and semi-arid regions. Plants tend to survive longer under drought stress through more efficient water use. Previous studies also found that changes in α were accompanied with variations in morphological traits along an aridity gradient [12]. Thus, we hypothesize that adjustment of morphological traits along the aridity gradient, which could be a better way to promote water use ability or enhance water use efficiency (WUE), will lead to variation in α . To test this hypothesis, we conducted field investigations along an aridity gradient from eastern to Western China. Our objectives were to test (1) whether WUE and α co-vary and; (2) whether individual traits drive variations in α and WUE along the aridity gradient.

MATERIALS AND METHODS

In the summer of 2009 and 2010, we collected field data from plant communities at nine sites along a natural aridity gradient in China (Table 1). Within each site, the sizes of different quadrat were established according to vegetation types (tree: 20 m, shrub: 10 m, herb: 2 m). The number of species, canopy cover and individual aboveground and belowground biomass of each species were measured in each quadrat. Aboveground and belowground biomasses were measured as in Dai et al. (2009) and Bai et al. (2010). Shrubs and herbs were harvested and biomass was determined in each quadrat. We measured the diameter at breast height (DBH) of trees, the height (H) and crown radius (r) 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. Aboveground biomasses of trees in Tianmu, Hangzhou and Dengfeng were estimated by H and DBH according to empirical equations. For Tianmu and Hangzhou, aboveground biomass of trees = $94.59 \times (\text{DBH}^2 \times \text{H})^{0.87}$ [16]; for Dengfeng, aboveground biomass of trees = $1.38 \times (\text{DBH}^2 \times \text{H})^{0.62}$ [17]. Aboveground biomass of trees in other sites was measured directly in harvested samples. Canopy coverage was calculated as the ratio of total canopy area to quadrat size. We dug out the roots of 5 samples in each sampling site and weighed their dry mass in labo-

ratory. Then we estimated the root mass of other species by the allometric relationships between the dry weight of roots and shoots of sample plants [18].

Stable carbon isotope ($\delta^{13}\text{C}$) has been widely used as a tool for the estimation of long-term WUE, and plants with higher $\delta^{13}\text{C}$ have higher WUE [19]. We sampled the leaves of dominant plant species used for the isotope analysis in each quadrat. Sampling procedure of leaves in each quadrat was the same as in Zheng and Shangguan's (2007). Leaves were oven-dried at 70° for 48h and grounded into 1-mm mesh sieve. Stable carbon isotope was measured on isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, USA). The $\delta^{13}\text{C}$ was determined using the following equation: $\delta^{13}\text{C} (\text{‰}) = (\text{R}_{\text{sample}} / \text{R}_{\text{standard}} - 1) \times 1000$, where R_{sample} and $\text{R}_{\text{standard}}$ are the $^{13}\text{C}/^{12}\text{C}$ ratio of the sample and of Pee Dee Belemnite standard, respectively. In this study, the $\delta^{13}\text{C}$ is mean value of dominant plant species in each quadrat.

The relationships of M-N, C-N and H-r were estimated by the reduced major axis (RMA) regression of \log_{10} -transformed data. Nonlinear relationships of α - $\delta^{13}\text{C}$, α -R/S, $\delta^{13}\text{C}$ -R/S, α - β and $\delta^{13}\text{C}$ -B were conducted by ordinary least square (OLS) regression.

RESULTS AND DISCUSSION

Our results confirmed that the scaling exponent (α) of the aboveground biomass-density relationship is not a constant, but rather changes across environmental gradients (Table 2). The α and δ increased with increasing drought stress, while β showed an inverse trend (Table 2). The α was significantly and positively correlated with $\delta^{13}\text{C}$ (Table 2, Fig. 1), which suggested the co-variation between WUE and α . The parameter β increased with decreasing $\delta^{13}\text{C}$ and δ , while the ratios of root to shoot (R/S) increased with increasing $\delta^{13}\text{C}$ and α (Table 2, Fig. 2).

Results from this investigation confirmed Dai et al. (2009)'s model prediction that β and δ could determine α in stressful environments (Table 2). Furthermore, α varies with WUE across the aridity gradient (Table 2, Fig. 1). We suggested that co-variation between α and WUE were

The main geographical and climatic conditions of the nine experimental sites. Aridity index (AI) = $\log(\text{MAE}/\text{MAP})$, where MAE is the mean annual evaporation and MAP is the mean annual precipitation. MAT is mean annual temperature

Sites	Parameters							Community characteristic	Dominant species
	Longitude	Latitude	Altitude(m)	MAT, °C	MAP, mm	MAE, mm	AI		
Tianmu	119°26'E	30°20'N	381	14.8	1390	1249	-0.05	Mixed montane	<i>Cunninghamia lanceolata</i> , <i>Castanopsis sclerophylla</i> , <i>Liquidambar formosana</i>
Hangzhou	120°06'E	30°14'N	263	16	1141	1275	0.05	Mixed montane	<i>Pinus massoniana</i> , <i>Castanopsis sclerophylla</i> , <i>Schima superba</i> , <i>Cyclobalanopsis glauca</i>
Dengfeng	112°55'E	34°30'N	616	10.2	563	1300	0.36	Evergreen montane	<i>Quercus acutidentata</i>
Lanzhou	103°53'E	35°52'N	1575	9.1	346	1342	0.59	Deciduous montane + shrub	<i>Sophora japonica</i> , <i>Ulmus pumila</i> , <i>Populus tomentosa</i> , <i>Euonymus japonicus</i>
Zhangye	100°38'E	38°46'N	1617	7	127.5	2047.9	1.21	Shrub	<i>Ajania fruticnlosa</i> , <i>Nitraria tangutorum</i>
Jiayuguan	97°49'E	39°46'N	2120	6	80	2149	1.43	Shrub	<i>Tamarix chinensis</i> , <i>Reaumuria soongorica</i> , <i>Salsola passerina</i>
Jiuquan	98°41'E	39°52'N	1379	8.2	67	3000	1.65	Shrub	<i>Nitraria tangutorum</i> , <i>Reaumuria soongorica</i>
Shulehe	96°05'E	40°34'N	1386	8.8	50	3000	1.78	Shrub	<i>Nitraria tangutorum</i> , <i>Ajania fruticnlosa</i> , <i>Reaumuria soongorica</i>
Guazhou	95°38'E	40°47'N	1250	8.8	45.7	3140.6	1.83	Shrub	<i>Nitraria sphaerocarpa</i> , <i>Ephedra przewalskii</i> , <i>Nitraria tangutorum</i>

Scaling exponent (α) of the aboveground biomass–density relationship at three climatic regions (humid area: aridity index (AI) < 0.36; semi-arid area: 0.36 < AI < 1.21; 1 arid area: AI > 1.21), as estimated by the RMA regression of log-transformed data. Predicted α was calculated according to Dai et al. (2009) equation. **R/S is root/shoot ratios**

Sites	Mean α	Mean β	Mean δ	α (predicted)	$\delta^{13}\text{C}$ (‰)	Mean R/S
Humid area	-1.74	1.34	0.05	-1.58	-28.60	0.25
Semi-arid area	-1.27	0.89	0.11	-1.29	-26.17	0.65
Arid area	-0.95	0.77	0.32	-0.94	-23.19	2.39

attributed to the varied morphological traits of plant responses to drought stress (Table 2, Fig. 2).

Plant allometric growth is considered as an adaptive trait, which could maximize the uptake of limiting resource and promote whole-plant growth in stressful environments [12]. Our results showed that δ and R/S increased with increasing drought stress (Table 2), suggesting that root competition becomes the determinant of plant spacing when the canopy starts to open up. According to recent studies, plants usually distribute a relatively high proportion to roots in nutrient-poor environments [20], suggesting that R/S may increase with decreasing water availability. Previous studies also showed that lateral root spreads increased with decreasing mean annual precipitation [21], which would enable plant to maximize uptake of soil water during drought stress. The extension of root drives the importance of competition from aboveground to belowground. Thus, self-thinning could be due to belowground competition for water resource under open canopy condition.

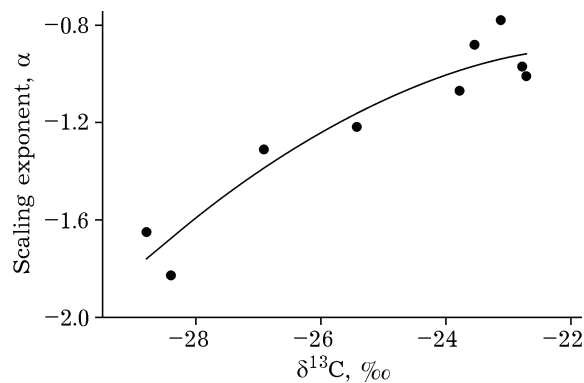


Fig. 1. Scaling exponent (α) of the aboveground biomass–density relationship increases with foliar stable carbon isotope ($\delta^{13}\text{C}$). $y = -7.28 - 0.61x - 0.01x^2$ ($r^2 = 0.87, P < 0.01$)

Plants compete primarily for light at wet sites, and rapid height growth is crucial for effective light interception [22]. For this reason, plants in such environments should have higher height for a given amount of radial extension. But in aridity area, light competition is usually less important than belowground

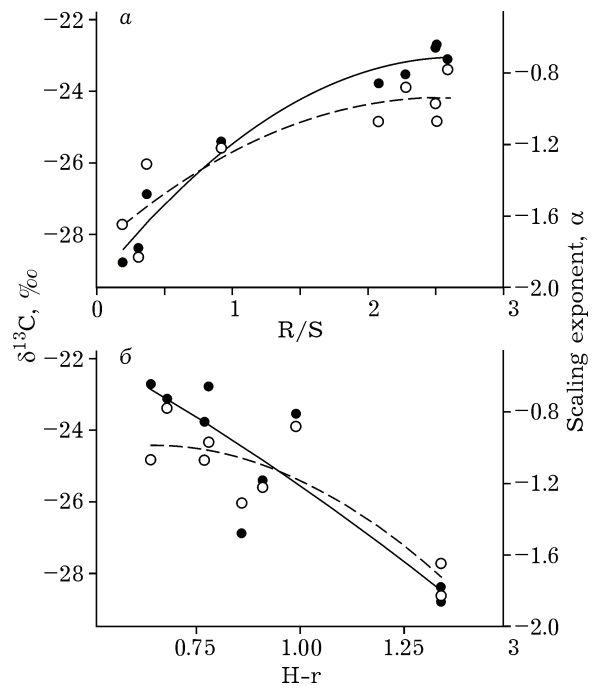


Fig. 2. *a* – both foliar stable carbon isotope ($\delta^{13}\text{C}$) (closed, solid line) and scaling exponent (α) of the aboveground biomass–density relationship (open, dash line) increase with the ratios of root to shoot (R/S). Formulas are $y = -29.31 + 4.71x - 0.89x^2$ ($r^2 = 0.96, P < 0.01$) and $y = -1.77 + 0.67x - 0.13x^2$ ($r^2 = 0.75, P < 0.01$) respectively for $\delta^{13}\text{C}$ line and α line. *b* – both $\delta^{13}\text{C}$ (closed, solid line) and α (open, dash line) decrease with the plant height-crown radius relationships (H-r). Formulas are $y = -19.12 - 4.82x - 1.63x^2$ ($r^2 = 0.68, P = 0.01$) and $y = -1.59 + 1.89x - 1.49x^2$ ($r^2 = 0.68, P = 0.01$) respectively for $\delta^{13}\text{C}$ line and a line for α line

competition for water [8], and the energy cost of vertical water transport may arise when water availability is low [12]. Our results showed that β decreased with increasing drought stress (Table 2), suggesting that plants should decrease height for enhancing WUE where water is more limiting than light.

Zhang et al. (2005) found that variation in α among different genotypes of *Arabidopsis thaliana* was due to different sensitive to *abscisic acid* (ABA). ABA is a well-known stress-inducible plant hormone, which regulates transpiration water loss and plant growth. Plants that are sensitive to ABA have smaller shoot height and larger R/S than ABA-insensitive plants do under drought stress [23]. Thus, the physiological traits affected α through their effects on the morphological traits which are associated with adaptation to drought.

ACKNOWLEDGEMENTS

This study was supported by Ministry of Science and Technology of China (2011AA100503) and Natural Science Fund of China (30871470).

REFERENCES

1. Damuth J. D. Common rules for animals and plants // Nature. 1998. Vol. 395. P. 115.
2. Enquist B. J. et al. Allometric scaling of plant energetics and population density // Nature. 1998. Vol. 395, N 163.
3. Dodds P. S. et al. Re-examination of the '3/4-law' of metabolism // J. Theor. Biol. 2000. Vol. 209. P. 9.
4. Darveau C. A. et al. Allometric cascade as a unifying principle of body mass effects on metabolism // Nature. 2002. Vol. 417. P. 166.
5. Kozlowski J., Konarzewski M. Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? // Funct. Ecol. 2004. Vol. 18. P. 283.
6. Brown J. H. et al. Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant // Funct. Ecol. 2005. Vol. 19. P. 735.
7. Morris E. C. Self-thinning lines differ with fertility level // Ecol. Res. 2002. Vol. 17. P. 17.
8. Deng J. M. et al. Plant mass-density relationship along a moisture gradient in north-west China // J. Ecol. 2006. Vol. 94. P. 953.
9. Chu C. J. et al. Balance between facilitation and resource competition determines biomass-density relationships in plant populations // Ecol. Lett. 2008. Vol. 11. P. 1189.
10. Pretzsch H. Species-specific allometric scaling under self-thinning: evidence from long-term plots in forest stands // Oecologia. 2006. Vol. 146. P. 572.
11. Clark J. S. Integration of ecological levels: individual plant growth, population mortality and ecosystem processes // J. Ecol. 1990. Vol. 78. P. 275.
12. Dai X. F. et al. Plant height-crown radius and canopy coverage-density relationships determine above-ground biomass-density relationship in stressful environments // Biol. Lett. 2009. Vol. 5. P. 571.
13. Bai Y. Y. et al. Variation in root:shoot ratios induced the differences between above and belowground mass-density relationships along an aridity gradient // Acta Oecol. 2010. Vol. 36. P. 393.
14. Zhang H. et al. Sensitivity of response to abscisic acid affects the power of self-thinning in *Arabidopsis thaliana* // Botanical Bulletin of Academia Sinica. 2005. Vol. 46. P. 347.
15. Zhang W. P. et al. The difference between above-and below-ground self-thinning lines in forest communities // Ecol. Res. 2011. Vol. 26. P. 819.
16. Zhang J. et al. Carbon storage by ecological service forests in Zhejiang Province, subtropical China // For. Ecol. Manage. 2007. Vol. 245. P. 64.
17. Liu Y. C. et al. Studies on biomass and net production of *Quercus acutidentata* forest in Baotianman Nature Reserve // Acta Ecologica sinica. 2001. Vol. 21. P. 1451.
18. Cheng D. L., Niklas K. J. Above-and below-ground biomass relationships across 1534 forested communities // Ann. Bot. 2007. Vol. 99. P. 95.
19. Zheng S. X., Shangguan Z. P. Spatial patterns of foliar stable carbon isotope compositions of C₃ plant species in the Loess Plateau of China // Ecol. Res. 2007. Vol. 22. P. 342.
20. Gedroc J. J. et al. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? // Funct. Ecol. 1996. Vol. 10. P. 44.
21. Schenk H. J., Jackson R. B. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems // J. Ecol. 2002. Vol. 90. P. 480.
22. King D. A. The adaptive significance of tree height // Am. Nat. 1990. Vol. 135. P. 809.
23. Yin C. Y. et al. Morphological and physiological responses of two contrasting Poplar species to drought stress and exogenous abscisic acid application // Plant Sci. 2004. Vol. 167. P. 1091.