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*Regular research paper*

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# INVARIANT ALLOMETRIC RELATIONSHIP BETWEEN ABOVE- AND BELOW-GROUND BIOMASS ALONG A MOISTURE GRADIENT IN NORTH –WEST CHINA

ABSTRACT: Biomass allocation pattern is an important plant characteristic which influences how plants respond to abiotic and biotic heterogeneity. Prior studies indicate that above-ground biomass scales nearly isometrically with respect to below-ground biomass regardless of environment or phyletic affinity. However, such rule has been mostly tested with data on trees and usually without drought stress. Given the importance of this predicted relationship, it should be evaluated for a wider range of species and environmental conditions. Variations of the above- and below-ground biomass ($M_A$ and $M_R$, respectively) were determined from five sites in north-west China, which compose a natural moisture gradient (aridity index ranging from 0.95 to 1.98). Model Type II regression protocols were used to compare the numerical values of $M_A$ *vs* $M_R$ scaling exponents (*i.e.* slopes of log-log linear relationships). The resulting five scaling exponents were indistinguishable and had a similar, nearly isometric slope (*i.e.* $M_A \propto M_R^{\approx 1.0}$). Significant variation was observed in the *Y*-intercepts of the five regression curves, because of the absolute differences in $M_A$ or $M_R$. These results support prior allometric theory, which reveals an isometric relationship between above- and below-ground biomass, and may provide a suitable method to estimate the regional below-ground biomass based on the direct above-ground measurements.

KEY WORDS: above- and below-ground biomass, allometry, isometric scaling, moisture gradient

## 1. INTRODUCTION

Biomass allocation pattern between above- and below-ground is an important plant traits in studies on the ecology and evolution of plants, and in global climate models, because it influences the functioning of terrestrial plants at all levels, ranging from individual growth and reproduction to the flow of mass and energy through entire communities (reviewed by Niklas 2006). Specifically, estimation of terrestrial vegetation biomass and carbon cycling requires a reliable means to assess below-ground biomass. Unlike the harvesting of above-ground biomass, it is laborious and time-consuming to obtain directly below-ground biomass through excavation (*e.g.* Brown 2002). It would thus be highly desirable to develop a general model which allows us to predict below-ground biomass from above-ground biomass.

Previous work indicated that above-ground biomass (shoot dry mass = leaf dry mass + stem dry mass, denoted by $M_A$) scaled nearly isometrically with respect to below-ground biomass (root dry mass, denoted by $M_R$) at both the individual level and the community level, regardless of environmental conditions (*i.e.* $M_A \propto M_R$) (Enquist and Niklas 2002, Niklas 2005, 2006, Cheng and Niklas 2007). This isometry is predicted from a strictly analytical approach to how plants annually partition their total body mass among leaf, stem and root mass ($M_L$, $M_S$ and $M_R$, respectively), and is believed to be the result of allometric constraints of evolution (Enquist and Niklas 2002). Predictions of such isometric relationship, however, have been mostly tested with data on forest plants, usually without drought stress (Enquist and Niklas 2002). Given the importance of this predicted relationship, it should be evaluated for a wider range of species and environmental conditions (Fang *et al.* 2001, Zens and Webb 2002, Robinson 2004). Therefore, investigation of such relationship of plants living in arid conditions where they are likely to be confronted with allometric constraints (*e.g.* arid habitat drives plants to allocate more biomass to root growth) will shed light on the existence of such general rule.

According to the optimal allocation theory, plants should allocate more resources to organs that capture the most limiting resources and less to organs that are involved in obtaining non-limiting resources (*e.g.* Bloom *et al.* 1985). When water is the driving force of biomass allocation in most arid or semiarid ecosystems, plants, for example, should allocate relatively more of their biomass to roots , relative to shoots. Therefore, it can be expected that an isometric relationship is found between $M_A$ and $M_R$ irrespective of water availability whereas the allometric constant (Y-intercept) differs among habitats with different water availability. However, current empirical evidence is inconsistent. For example, Deng *et al.* (2006) studied the relationship between biomass and plant density ($N$) in natural communities along a moisture gradient and indicated that the scaling exponents for $M_A$ *vs* $N$ decreased with natural moisture levels, whereas scaling exponents for $M_R$ *vs* $N$ shared a common nearly predicted value of -4/3. Above results might imply that the scaling exponent for $M_A$ *vs* $M_R$ relationship would decrease with increasing the aridity index.

Here, we collected biomass data of shrub-dominated communities at five sites along a natural moisture gradient in north-west China to test whether an isomeric above- and below-ground biomass allocation pattern exists and is insensitive to aridity conditions.

## 2. MATERIALS AND METHODS

The study was carried out in late summer from August to September 2005 in arid or semi-arid regions in the northwest China. Five sites were selected along a moisture gradient, reaching from Baiyin (central of Gansu province) to Ejina, westest of Inner Mongolia (Fig. 1). The transect changes in the annual average precipitation ($P$) amounted from 209.00 mm to about 38.24 mm, while the annual average evaporation ($E$) from almost 1852.0 mm to 3631.9 mm (Table 1). All sites have similar rainfall seasonality, with a rainfall maximum in July to September, and a rainfall minimum in May (Chen *et al.* 2007). The aridity index ($G$, calculated as the form: $G = \log_{10}(E/P)$) for five sites ranges from 0.95 to 1.98, which composes a moisture gradient. The plants along this moisture gradient are composed mainly of shrub-dominated communities, and the species diversity is relative-

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

| Parameters | Site | | | | |
|---|---|---|---|---|---|
| | Baiyin | Linze | Minqin | Jinta | Ejina |
| Latitude | 36°43′N | 39°19′N | 38°34′N | 39°56′N | 40°52′N |
| Longitude | 104°11′E | 100°12′E | 102°58′E | 98°39′E | 102°11′E |
| Annual mean temperature (°C) | 8.0 | 7.6 | 7.6 | 7.6 | 8.0 |
| Annual mean precipitation (mm) | 209.0 | 116.8 | 110.0 | 59.5 | 38.2 |
| Annual mean potential evaporation (mm) | 1852 | 2390 | 2604 | 2539 | 3632 |
| Aridity index | 0.95 | 1.31 | 1.37 | 1.63 | 1.98 |

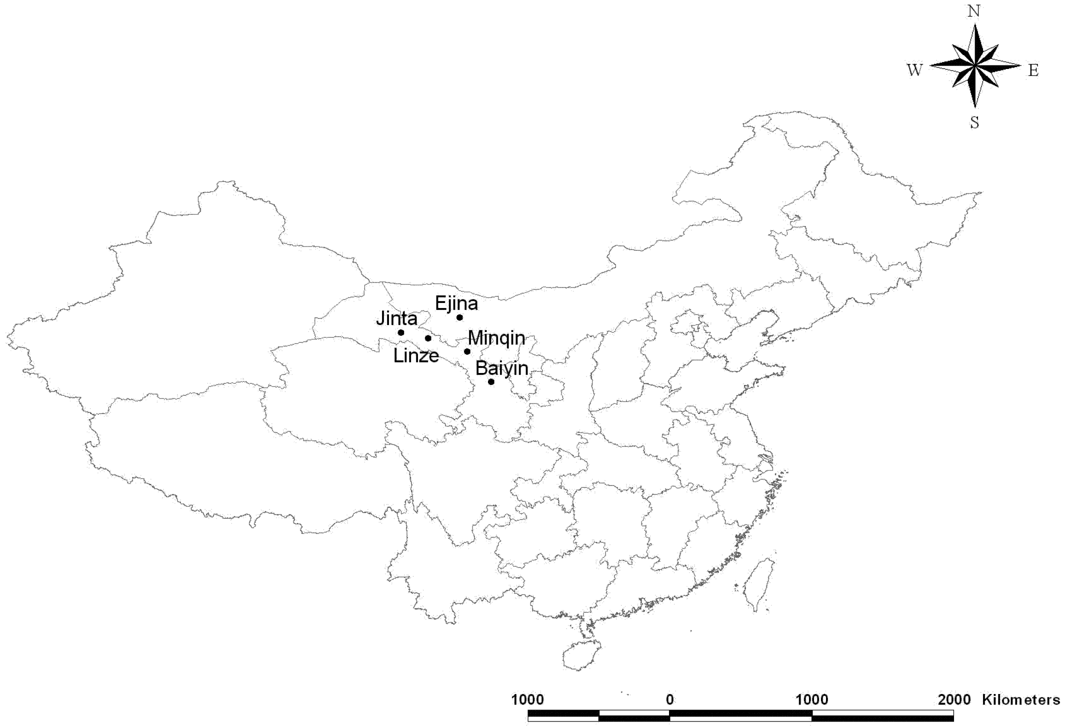

Fig. 1. The map of the sampling moisture gradient in this study.

ly low. Square plots of 10 × 10 m, 5 × 10 m, 2 × 2 m were selected according to the plant types, including shrubs, sub-shrubs, perennials and annual grasses as they exist, *e.g.* 2 × 2 m was selected for annual grasses, and 10 × 10 m for shrubs. The data of inter-specific variations in above- and below-ground biomass at the five sites were determined.

Plants were harvested and fresh above- and below- ground biomass was determined. The below-ground biomass was harvested using the soil monolith method (Deng *et al.* 2006). Sub-samples of above- and below-ground material were used to determine fresh to dry mass ratio, and then weighed after oven-drying at 85°C for 72 hours. The total dry biomass for each sample was calculated using the dry/wet mass ratio and the total fresh weight. Then the average above- and below-ground biomass for every species was determined.

Data for $M_A$ and $M_R$ (original g per individual) for the different species were $\log_{10}$-transformed. Since Model Type II (reduced major axis, RMA) regression protocol is appropriate when the purpose is to estimate the functional relationship between two variables (Niklas 1992), RMA regression protocols were used to determine the slope and $Y$-intercept of log-log linear functions, *i.e.*, $\alpha_{RMA}$ and log $\beta_{RMA}$, respectively. The software package "Standardised Major Axis Tests and Routines ((S)MATR)" (Warton and Weber 2002; Falster *et al.* 2003) was used to determine whether the numerical values of $\alpha_{RMA}$ for log $M_A$ *vs* log $M_R$ differed between contrasted data subsets. This software package was used to provide the Model Type II equivalent of ordinary least squares (OLS) standard analyses of covariance (ANCOVA). The significance level for testing slope heterogeneity was $P> 0.05$ (*i.e.*, slope heterogeneity was rejected if $P> 0.05$).

## 3. RESULTS

Across all five data sets, the scaling exponents of the relationship between above- and below-ground biomass nearly equaled to unity (Fig. 2; Table 2). Numerically, the lowest scaling exponent was observed for the Minqin data set and the highest for Ejina data set (*i.e.*, $\alpha_{RMA} = 0.909$ and 0.962, respectively). We were particularly interested in determining if there were significant differences in the

Table 2. (S)MATR reduced major axis regression slopes and y-intercepts ($\alpha_{RMA}$ and log $\beta_{RMA}$, respectively) for log10-tranformed data of arid or semi-arid plant species above- and below-ground biomass ($M_A$ and $M_R$, respectively) (original units: g dry mass per individual). Sites – see Fig.1 and Table 1.

| Site | $\alpha_{RMA}$ (95% CI) | log $\beta_{RMA}$ (95% CI) | $r^2$ |
|---|---|---|---|
| Baiyin | 0.918 (0.844, 0.997) | 0.212 (0.071, 0.354) | 0.930 |
| Linze | 0.957 (0.856, 1.069) | 0.133 (-0.065, 0.332) | 0.892 |
| Minqin | 0.909 (0.821, 1.007) | 0.176 (-0.12, 0.476) | 0.897 |
| Jinta | 0.959 (0.883, 1.042) | 0.096 (-0.10, 0.294) | 0.933 |
| Ejina | 0.962 (0.907, 1.021) | 0.214 (0.058, 0.370) | 0.989 |
| All data | 0.941 (0.910, 0.972) | 0.171 (0.093, 0.248) | 0.939 |

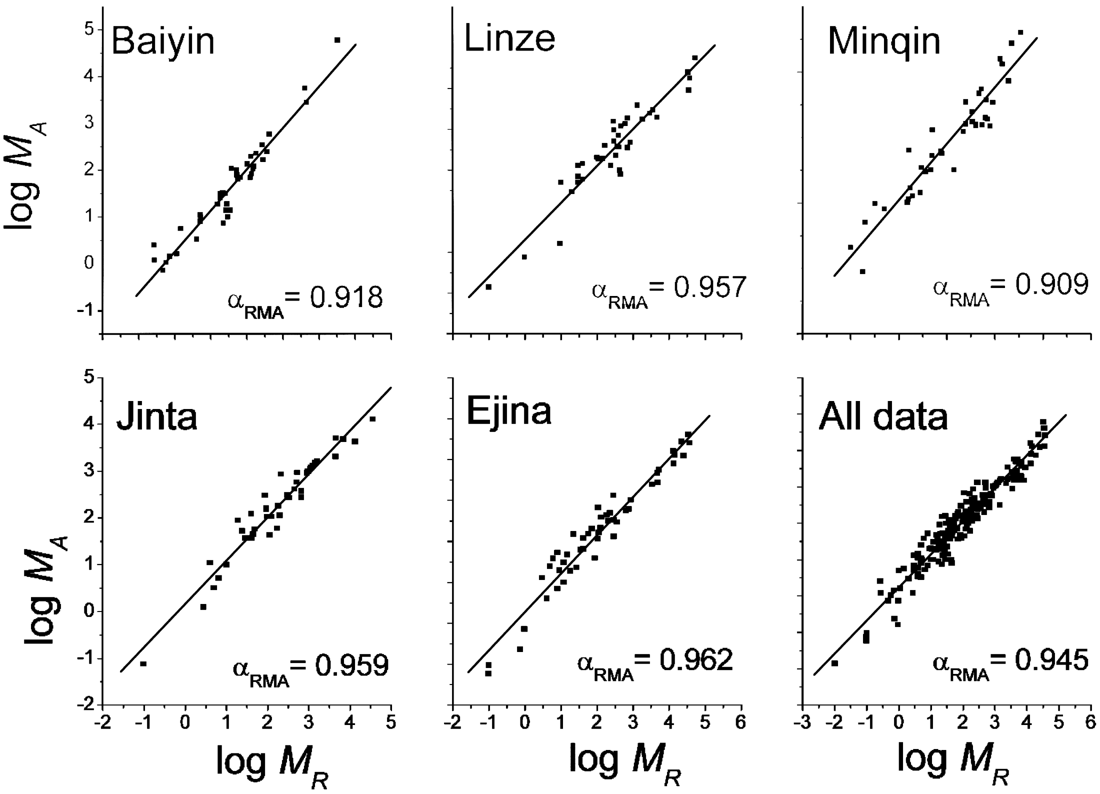

Fig. 2. Bivariate plot of log10-transformed data for dry above-ground mass and dry below-ground mass ($M_A$ and $M_R$, respectively). All sites have a slope statistically indistinguishable from 1.0. Regression statistics are given in Table 2.

numerical value of the slopes along the moisture gradient. RMA 95% CI overlaps and (S) MATR analyses indicated that the slopes were not significantly different and shared a nearly isometric slope (*i.e.* common slope: $\alpha_{RMA} = 0.945$, 95% CI = $0.912 \le \alpha_{RMA} \le 0.980$; test for the homogeneity of regression slopes, $F = 1.634$, $P = 0.803$).

Because the absolute amounts of $M_A$ *vs* $M_R$ depends on the numerical values of the *Y*-intercepts of regression curves, *i.e.* log $\beta_{RMA}$, we tested the homogeneity of log $\beta_{RMA}$ of this transect. Substantial variation in log $\beta_{RMA}$ was observed across the five different $M_A$ *vs* $M_R$ regression curves ($P < 0.05$; Table 2), suggesting that the absolute values of $M_A$ vary substantially with respect to $M_R$ at different water conditions. However, irrespective of the difference in log $\beta_{RMA}$, the $M_A$ scaled as 0.941 power of $M_R$ across the entire data sets (Fig. 2; Table 2), which still did not significantly deviate from 1.0.

## 4. DISCUSSION

Our analyses show that a nearly isometric scaling relationship between above- and below-ground biomass holds true along the natural moisture gradient (Table 2; Fig. 2). We have shown that the numerical values of the scaling exponents governing this relationship are numerically similar or indistinguishable from those reported for the forest communities, supporting the relations predicted by the isometric model (Enquist and Niklas 2002, Niklas 2005, 2006, Cheng and Niklas 2007). However, significant differences in the absolute above- or below-ground biomass are reflected in the numerical differences in the allometric constants (*Y*-intercepts of log-log linear regressions) associated with this isometric pattern (Table 2), which agrees with prior allometric studies that environment conditions may affect the allometric constant but not the scaling exponent (*e.g.* Cheng and Niklas 2007). Intraspecific biomass allocation patterns reflect the phenotypic plasticity of a particular environmental condition, which provide individual allometric trajectories terminating with adult forms that represent the end-points in interspecific scaling relationships, whereas the inter-specific biomass allocation patterns reflect a much broader range of plant forms and phenotypic reaction norms. According to the consistence of isometric scaling relationship between above- and below-ground biomass at the present paper (Table 2; Fig. 2) and that of desert shrub *Larrea tridentata* (D.C.) Cov. reported by Allen *et al.* (2008), it is reasonable to suggest that such rule exists in the dry conditions at both the level of individual species and the level of functional species groups.

It is well known that plants should allocate resources to increase their uptake of the resource that is most limiting growth (*e.g.* Bloom *et al.* 1985, Hunt and Lloyd 1987, McConnaughay and Coleman 1999, Poorter and Nagel 2000, Weiner 2004). Under drought stress, plants often show an open canopy and increased ratio of root to above -ground biomass (Zhang *et al.* 1995; Li 2000). Although the allometric constants, to a certain extent, can be interpreted as the ratios of above- to below-ground biomass (*i.e.* $M_A : M_R^{\approx 1.0} \propto \log \beta_{RMA}$), our results showed no significant correlation between the allometric constants and aridity index ($P > 0.05$), which could be attributed to the following two factors. First, plants growing in arid habitats show a positive feedback between biomass and resource availability, resulting in a process of local facilitation to set against the background of overall control by water availability. For example, the interception of rain and dust by plants is related to the plant height, canopy, and existence of other plants (*e.g.* Tongway *et al.* 1989, Schlesinger and Pilmanis 1998, Scanlon *et al.* 2007). Second, plants develop diverse strategies to adapt to the drought stress. For example, shrubs can use the deeper soil water, producing more below-ground biomass, whereas, annual grasses utilize the upper layers of the soil water, thus obtaining more above-ground biomass (Gill *et al.* 2002). Meanwhile, it seems that a high ratio of above- to below-ground biomass is not typical of desert plants; it may be more closely related to certain life forms or temperature regimes than aridity (Noy-Meir 1973). Therefore, it is reasonable to expect that there was no correlation between aridity and the allometric constants.

The findings by Deng *et al.* (2006) that indicate a nearly -4/3 relationship of belowground biomass, $M_R$ to plant density, $N$, but a decreasing scaling exponent for aboveground biomass, $M_A$, and $N$ along a natural moisture level, suggest that $M_A$ *vs* $M_R$ may change with moisture. We argue that the inconsistency between Deng *et al.* (2006) and the present paper at least in part resulted from the different aims for the two studies. It is generally believed that biomass-plant density relationship occurs and appears to be the consequence of negative interactions between individuals (*i.e.* competition for water) (*e.g.* Yoda *et al.* 1963, White 1985). However, more recent experimental studies have discovered that positive interactions, *i.e.* one species enhances the performance of another, are thought to be of great importance in arid and semi-arid areas (Whitford 2002, Cheng *et al.* 2006). Bertness and Callaway (1994) hypothesized that the importance of facilitation in plant community organization increased with abiotic stress and with decrease in the relative importance of competition. Presumably then, the biomass-density relationship might change along a moisture gradient as reported by Deng *et al.* (2006).

The biomass estimates for arid region are calculated usually from average ratio of below- to above-ground biomass. Because the ratio of $M_R$: $M_A$ increases steeply for small plants and then approaches an asymptote, as plant biomass increases (*e.g.* Zens and Webb 2002) it is difficult to compare ratio among different plant species of different total biomass. The concern arises about methods bias confounding the biomass results for arid conditions. Our findings defined the isometric rule for above- and below-ground biomass partitioning along the moisture gradient. Indeed, one of the important applications of the scaling relationship reported here is the estimation of regional below-ground carbon sequestration for arid or semi-arid ecosystems because above- ground biomass explains more than 89% of variations of below-ground biomass (Table 2). Nevertheless, it is worth noting that absolute above- or below-ground biomass is influenced by many factors (*e.g.* temperature, nutrition). Hence, more data are required to test and modify the isometric pattern.

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