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ORIGINAL PAPER

Variation in individual biomass decreases faster than mean biomass with increasing density of bamboo stands

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Abstract The total biomass of a stand is an indicator of stand productivity and is closely related to the density of plants. According to the self-thinning law, mean individual biomass follows a negative power law with plant density. If the variance of individual biomass is constant, we can expect increased stand productivity with increasing plant density. However, Taylor's power law (TPL) that relates the variance and the mean of many biological measures (e.g. bilateral areal differences of a leaf, plant biomass at different times, developmental rates at different temperatures, population densities on different spatial or temporal scales), affects the estimate of stand productivity when it is defined as the total biomass of large plants in a stand. Because the variance of individual biomass decreases faster than mean individual biomass, differences in individual biomass decline with increasing density, leading to more homogeneous timbers of greater economic value. We tested whether TPL in plant biomass holds for different species and whether the variance of individual biomass changes faster than the mean with increasing stand density. The height, ground diameter and fresh weight of 50 bamboo species were measured in 50 stands ranging from 1 m by 1 m to 30 m by 30 m to ensure more than 150 bamboos in every stand. We separately examined TPL in height, ground diameter, and weight, and found that TPL holds for all three biological measures, with the relationship strongest for weight. Using analysis of covariance to compare the regression slopes of logarithmic mean and variance against the logarithm of density, we found that the variance in individual biomass declined faster than the mean with increasing density. This suggests that dense planting reduced mean individual biomass but homogenized individual biomass. Thus, there exists a trade-off between effective stand productivity and stand density for optimal forest management. Sparse planting leads to large variation in individual biomass, whereas dense planting reduces mean individual biomass. Consequently, stand density for a plantation should be set based on this trade-off with reference to market demands.

Keywords Bamboo · Linear fitting · Self-thinning law · Taylor's power law · Variance

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Introduction

It is important to understand the temporal and spatial variability of a population to provide theoretical guidance to the management of species. To this end, many have studied and verified a number of power laws that govern the variation in population density (Cohen et al. 2012). Taylor's power law (TPL) has been used to describe the relationship between the variance (V) and the mean (M) of population densities, and takes the form of $V = \alpha{\cdot}M^{\beta}$ (Taylor 1961), where α represents a constant, and β is an empirical exponent ranging from 1 to 3 (Taylor 1981; Anderson et al. 1982; Ballantyne and Kerkhoff 2007; Kaltz et al. 2012; Giometto et al. 2015; Cohen and Xu 2015; Xiao et al. 2015; Shi et al. 2016, 2018; Tippett and Cohen 2016). Taylor's power law has been applied and verified widely in many disciplines such as botany, ecology, economics, entomology, epidemiology, meteorology, and physics (Walgenbach 1994; Yamamura 2000; Eisler et al. 2008; Kaltz et al. 2012; Tippett and Cohen 2016; Cheng et al. 2017; Cohen et al. 2017a; Lin et al. 2018; Shi et al. 2017a, b, 2018). Multiple biological and ecological constraints affect the exponent β of TPL. For instance, Shi et al. (2016) demonstrated that the dispersal distance from parent plants affects the exponent of TPL with reference to offspring distribution. The exponent of TPL was largest for short-distance dispersal while other capabilities of dispersal in parent plants reduced the exponent of TPL. There is also TPL for the variance and the mean of crop biomass at different times (Shi et al. 2017a), with the variation in crop biomass the largest for mature crops. Lin et al. (2018) confirmed that TPL also holds for the developmental rate of two dwarf bamboo species growing at different air temperatures at the seeding emergence and leaf-unfolding stages, and the same was found for insects (Shi et al. 2017b). However, it remains unclear how TPL of plant biomass is related to other laws of plant dimensions such as leaf area, stem diameter and tree height. Cheng et al. (2017) analyzed TPL with reference to the internode variables for a bamboo *Pseudosasa amabilis*, including internode diameter, length, thickness, and weight, and found that the physical dimensions of these measures could significantly affect the goodness of fit to the log–log linear regression of TPL. TPL for weight yielded a better fit than did other parameters because weight (and biomass) represents the highest physical dimension among these measures. However, this conclusion was drawn based on a single plant organ (namely the internode of bamboos).

The self-thinning law (STL) describes another power-law relationship between the mean biomass (M) of a population and its density (D; the number of individuals per unit area): $M = c{\cdot}D^{d}$, where c is a constant and d is an empirical exponent with value of − 3/2 (Yoda et al. 1963) that varies slightly for different species. STL usually holds only for single-species forests and can be used to compare the space use of different populations (Franco and Kelly 1998; Enquist and Niklas 2001; Vanclay and Sands 2009; Cohen et al. 2016, 2017b; Liu et al. 2016). Few studies examined STL for a mixture of species but Li et al. (2000) theoretically demonstrated the possibility of STL for closely related species. If both TPL and STL adequately describe population variability, a third predictive power law, the variance-density allometry (VDA), can be established by combining TPL and STL, which can be used for testing the relationship between variance in a specified morphological measurement and population density. For example, Cohen et al. (2016) combined TPL and STL to test whether the variance-density allometry holds in 250 plots of New Zealand mountain beech trees over three decades on different spatial scales. They found that a natural stand with a single species obeyed the three power laws while surveys on larger spatial scales increased the exponent of TPL. Shi et al. (2015) found that there is a power-law relationship between the mean of total leaf areas of four *Indocalamus* species and their spatial densities (i.e. the number of each plant species per unit area), showing a reduction of mean leaf area with increasing density. Liu et al. (2016) found that, with increasing numbers of bamboos per unit area, mean ground diameter and mean fresh weight declined in 50 bamboo species, and the log-transformed data fitted well to a linear equation. Although TPL, STL and VDA hold for single-species forests (Cohen et al. 2016), the evidence for closely related species within the same taxonomic group remains lacking. Moreover, if the exponent of STL is smaller than that of VDA, the variance of individual biomass should decline faster than mean individual biomass with increasing stand density. This is important for forest management as a small variance of individual size (such as for diameter at breast height [DBH], tree height, or biomass) indicates a greater degree of evenness in trees, a factor strongly influencing the commercial value of timber. However, dense stands might yield lower individual biomass and consequently have lower stand productivity.

Bamboos are a unique group of species unlike both herbaceous plants and trees. Bamboos grow as woody grasses of the Graminaceae family and are represented by 1439 species of 116 genera (Bamboo Phylogeny Group 2012). Bamboos are widely distributed worldwide; however, they are most abundant and diverse in Asia, where they are used by 2.5 billion people for fibers or industrial materials, and as important sources of bioenergy, food products, construction materials, and a component of environment management regimes (Scurlock et al. 2000; Wei et al. 2017). The height growth of bamboos is much faster than for most plant species (Shi et al. 2017a). Some bamboo species are capable of growing over one meter per night during the stage of rapid growth (Wei et al. 2018). Bamboos generally bloom infrequently, or exhibit unusual flowering habits owing to self-regulating mechanisms or to triggering by environmental cues (Franklin 2004). Studies of fast growth among bamboos and of flowering mechanisms on both macroscopic and microscopic scales has attracted growing interest (Franklin 2004; Yuan et al. 2017; Wei et al. 2017, 2018). Recent work focused on the geographic distribution of different bamboo species and on variations in biomass and growth patterns. The mathematical analysis of population dynamics has not been equally emphasized, with the exception of the TPL morphmetrics of bamboo internodes (Inoue 2013; Cheng et al. 2017). Although the self-thinning relationship between stand density and plant size has been verified for different bamboo species (Liu et al. 2016), TPL has not been tested with reference to ground diameter or plant height or weight. We tested whether TPL and VDA would hold for the bamboo data published in Liu et al. (2016). We also assessed whether TPL fit plant weight (a good indicator for biomass) better than it fit other parameters (Cheng et al. 2017). The exponents of STL and VDA were also compared to evaluate the effects of plant density on these two power laws. We chose bamboos rather than trees as Bambusoideae has many species and large variation in the body size of different bamboo species. Thus, we were able to test these three power laws using different bamboo species.

Materials and methods

Study area

From three distinct areas we collected fifty bamboo species that were characterized by rapid growth in height. Twelve bamboo species were collected in Dayu Scenic Bamboo Garden, Jiangdu City, Jiangsu Province, China (N32°28′, E119°38′). This region has mean annual temperature of 15.7 °C and mean annual rainfall of 1020 mm. Sixteen bamboo species were collected from the Bamboo Garden at Nanjing Forestry University in Jurong City, Jiangsu Province, China (N32°07′, E119°13′). This area has mean annual temperature of 15.5 °C and mean annual rainfall of 1099 mm. The remaining 22 bamboo species were collected from Bamboo Expo Park in Anji City, Zhejiang province, China (N30°37′, E119°41′) where mean annual temperature is 15.0 °C and mean annual precipitation is 1350 mm.

Data acquisition

We collected the stems of healthy, mature bamboo plants (most over 15 years old), and growing in areas with minimal anthropogenic disturbance. Then we sampled different bamboo stands in quadrats ranging in size from 1 × 1 m to 30 × 30 m, to ensure that the number of bamboos in a quadrat could exceed 150 individuals for each species. During the early growth stage, the primary thickening and height growth is completed but above-ground biomass continues to accumulate during later growth stages (Dai 2002; Pu and Du 2003). Therefore, in each sampled stand, height and ground diameter were measured on stems selected and cut from the first node without adventitious roots present from May to October in 2014. As moisture content is an important component of stem weight, fresh weight was used to investigate the three power laws (Cheng et al. 2017; Liu et al. 2016). Immediately after the culms were cut off, we measured their fresh weight. Thus, the water loss could be neglected.

Statistical methods

For a power-law function $y = \alpha x^{\beta}$, we can use the natural logarithm to convert the non-linear equation to a linear equation: $\ln y = \ln \alpha + \beta \ln x \Leftrightarrow y' = a + bx'$, where $y' = \ln y$, $x' = \ln x$, $a = \ln \alpha$, and $b = \beta$. Linear regression based on the least-squares method was used to estimate parameters a and b. The model parameters and their 95% confidence intervals in accordance with TPL, STL and VDA, and with reference to ground diameter, height and fresh weight were computed by using the above method. To test whether weight fit a TPL relationship better than the other two measures, the coefficient of determination (R^2) was used to compare the goodness of fit for the three linear regression equations. Although the residual sum of squares (RSS) and the root mean square error (RMSE) both reflect goodness of fit, they are both affected by the absolute value of data. If the three data sets have different units, it is inappropriate to use RSS or RMSE for comparison. To compare differences in the exponents of STL and VDA, we used covariance analysis. The statistical software R was used to for linear regression and covariance analyses (version 3.2.2, R Core Team 2015). Unless otherwise noted, alpha levels for all statistical comparisons were 0.05.

Results

Comparison in TPL relationships among three measures of bamboos

Table 1 lists the fitted results for TPL with reference to ground diameter, height and fresh weight. The three slopes were all statistically significant, and their 95% confidence intervals all included 2. The power-law relationship between mean and variance of fresh weight ($R^2 = 0.98$) was stronger than that for either ground diameter ($R^2 = 0.90$) or height ($R^2 = 0.87$). The log-transformed data of variance for fresh weight fitted the straight regression line better than did the other two measures (Fig. 1).

STL and VDA relationships in fresh weight of bamboos

The estimates of a and b for STL were 2.50 ± 0.23 and − 1.17 ± 0.07, respectively (Table 1), and the corresponding 95% confidence intervals for these two parameters were (2.03, 2.97) and (− 1.30, − 1.04). The coefficient of determination of the linear regression on STL was 0.87. As expected, the mean of individual biomass for various bamboo species decreased with increasing population density (Fig. 2).

The variance of population densities decreased with increasing population density, and was proportional to the mean biomass to a specific power (Fig. 2). The estimates of a and b were 3.97 ± 0.49 and − 2.38 ± 0.14 with 95% confidence intervals of (2.99, 4.95) and (− 2.65, − 2.10), respectively. The coefficient of determination of the linear regression of density on variance was 0.86 (Table 1). The theoretical straight lines of STL and VDA intersected. As indicated on the left side of the intersection, the red solid line representing the variance of population density plotted above the dark dashed line representing mean biomass per individual. The opposite trend occurred on the right side of the intersection. Analysis of covariance showed that there was a significant difference between the exponent of STL and that of VAD (Table 2), demonstrating that the intersection indeed existed when the number of bamboos per unit area reached 3.4 m^{-2}. At the intersection, the mean of individual fresh weight equaled the variance of fresh weight (= 2.9 kg; Fig. 2). For most bamboo species, variance was lower than mean individual biomass.

Residual standard error: 1.707 on 97 degrees of freedom, $R^2 = 0.7960$, $R^2_{\mathrm{adj}} = 0.7917$, $F_{2,\ 97} = 189.2$, and $P < 0.001$. Here, 'ln (density)' denotes the effect of ln (density) on the density-mean power law (i.e. self-thinning law, STL), and the estimate of slope is − 1.77 ($P < 0.001$) which implies a significant influence of ln (density) on log (mean weight); the estimate of slope of 'Law: VDA' is equal to − 2.27 ($P < 0.001$), showing that there is a significant difference between two exponents of STL and VDA.

Discussion

TPL was initially used to describe the variance-mean relationship of insect population densities at different spatial and temporal scales (Taylor 1961). It also applies to other disciplines such as crop dry weight at different investigation times (Shi et al. 2017a, b), insect and plant developmental rates at different temperatures (Shi et al. 2017b; Lin et al. 2018), internode weight of bamboos (Cheng et al. 2017), leaf bilateral asymmetry (Shi et al. 2018; Wang et al. 2018b), UK crime reports (Hanley et al. 2014), traffic of Internet routers, trading activity of stock markets and weekly precipitation of weather stations (Eisler et al. 2008). Cheng et al. (2017) compared the fitted results in TPLs using internode length, diameter, volume and weight and found that the TPL of weight is the strongest. Shi et al. (2017a) confirmed that TPL of dry weight for several crops is stronger than TPL of crop height. It appears that biomass is a good measure for examining TPL on a variety of spatial or temporal scales. Our results were in accordance with the aforementioned

Table 1 Fitted results for the variance-mean, mean-density, and variance-density power law relationships for fifty bamboo species

Power law	Estimate		
	Intercept ± SD (95% confidence interval)	Slope ± SD (95% confidence interval)	R^2
$V_{\mathrm{GD}} \sim M_{\mathrm{GD}}$	− 2.73 ± 0.44 (− 3.61, − 1.84)	2.00 ± 0.10 (1.80, 2.20)	0.90
$V_{\mathrm{H}} \sim M_{\mathrm{H}}$	− 2.74 ± 0.15 (− 3.03, − 2.44)	1.86 ± 0.11 (1.65, 2.08)	0.87
$V_{\mathrm{W}} \sim M_{\mathrm{W}}$	− 1.12 ± 0.10 (− 1.32, − 0.91)	2.01 ± 0.04 (1.93, 2.10)	0.98
$M_{\mathrm{W}} \sim D_{\mathrm{W}}$	2.50 ± 0.23 (2.03, 2.97)	− 1.17 ± 0.07 (− 1.30, − 1.04)	0.87
$V_{\mathrm{W}} \sim D_{\mathrm{W}}$	3.97 ± 0.49 (2.99, 4.95)	− 2.38 ± 0.14 (− 2.65, − 2.10)	0.86

V represents the variance; *M* represents the mean; *D* represents the density; the subscripts GD, H and W represent ground diameter, height and fresh weight of bamboos, respectively

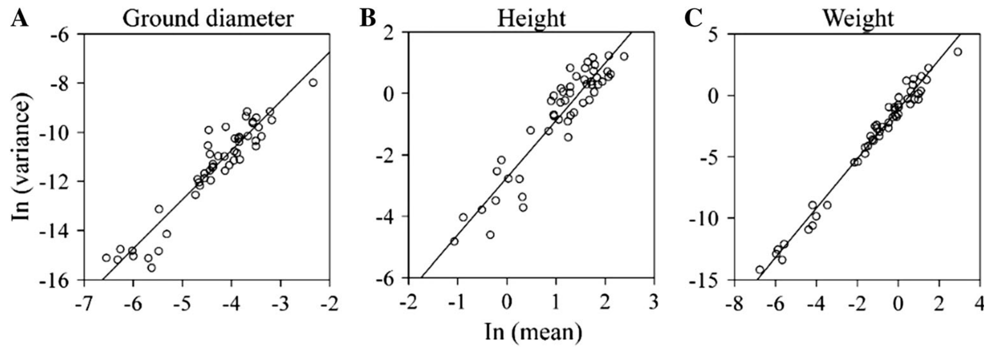

Fig. 1 Variance-mean power law relationships of three measures (diameter ground, height and fresh weight) for fifty bamboo species on the log–log scale

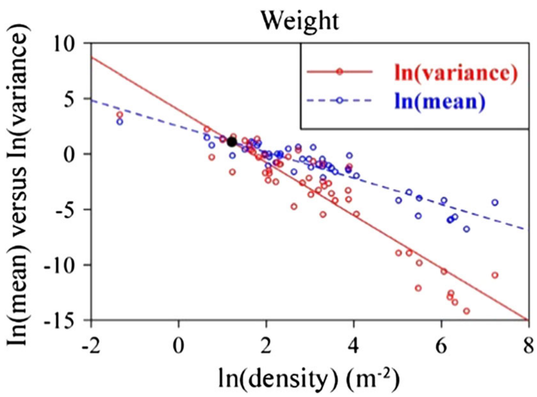

Fig. 2 Comparison between the mean-density power law (STL) and variance-density power law

Table 2 Results of the analysis of covariance for the density-mean and density-variance power-law relationships

Coefficients	Estimate	SE	*t*	*P*
Intercept	4.37	0.39	11.32	< 0.001
ln (density)	− 1.77	0.10	− 18.28	< 0.001
Law: VDA	− 2.27	0.34	− 6.65	< 0.001

reports. TPL applied to bamboo fresh weight yielded a stronger fit than did TPL when applied to other measures (namely ground diameter and height of bamboo).

There are different explanations for the emergence of TPLs, especially for those whose exponents range from 1 to 2 (Taylor 1981; Ballantyne and Kerkhoff 2007; Kilpatrick and Ives 2003; Cohen and Xu 2015; Giometto et al. 2015; Shi et al. 2016; Xiao et al. 2015). The debate on the emergence of TPLs centers around whether it is a statistical phenomenon from sampling skewed distributions (Cohen and Xu 2015; Xiao et al. 2015) versus whether it reflects biological mechanisms (Ballantyne and Kerkhoff 2007; Kilpatrick and Ives 2003; Shi et al. 2016). But these two views are not contradictory. Many biological measures exhibit skewed rather than normal distributions yet their distributions fit TPL. An example is the diameter at breast height of moso bamboos (Cheng et al. 2015), which is skewed yet conforms to TPL. The deviation of plant biomass from a normal distribution is likely related to the spatial distribution of soil nutrients. Soil nutrients are highly aggregated and can affect the distribution of individual biomass of plants (Shi et al. 2015). Spatial clustering can result in a power-law relationship between means and variances (Horne and Schneider 1995). In our opinion, TPL holds in other non-biological areas because there might exist similar skewed distributions.

Although STL, another closely related power law, describes the mean-density allometry, few studies have combined TPL with STL to generate the variance-density allometry (but see Cohen et al. 2016). However, Cohen et al. (2016) mainly emphasized the effect of spatial scale on the estimate of the TPL exponent. The comparison between the exponent of VDA and that of STL has been overlooked. Our results illustrate an intersection between VDA and STL, where the variance is equal to the mean. Notably, for about five bamboo species, variance of fresh weight is larger than the mean (indicating an over-dispersed distribution); however, for most species, the distributions of fresh weights are uniform and/or random because the variance is less than the mean (Hanski 1987; Horne and Schneider 1995). Qin et al. (2018) reported that the distributions of large individuals for four dwarf bamboo species are random and independent of the distributions of small individuals. Our study showed that with increasing density the variance declined faster than did the mean, indicating more uniform individual biomass. In contrast, at densities below carrying capacity, large variation in individual biomass can be expected (Qin et al. 2018; Wang et al. 2018a). However, even when a population has reached its carrying capacity, this does not necessarily suggest that all individuals have similar biomass. Instead, the biomass distribution could then reflect the spatial distribution of soil nutrients. In this case, the exponent of TPL might vary with population density (Kilpatrick and Ives 2003). To this end, the effect of spatial scales on the exponent of TPL might be attributable to differences in spatial distribution of soil nutrient at varying scales.

Few studies have examined different species to test STL and TPL. We examined 50 bamboo species to quantify STL and TPL for ground diameter, height, and fresh weight. The power law fitted fresh weight better than it fit ground diameter or height, with data points approximating a theoretical straight line of TPL on the log(mean weight)-log(variance of weight) plot. Based on TPL and STL, the variance-density allometry was demonstrated to hold for 50 bamboo species. The exponent of STL was greater than that of VDA. Because these two exponents were negative values, with increasing density the variance declined faster than the mean. For most bamboo species, the variance in weight is less than the mean, implying that the distribution of individual biomass is random. Our study suggests that a reasonable plantation density should reduce the variation in timber biomass. This merits further study to determine whether the conclusion applies also to trees.

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Author's contributions PS and GGW designed the experiment; PS analyzed the data; GL and FW carried out field experiment; GL, CH, MC, LSP and PS wrote the manuscript; GL and MC contributed equally to this work.

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