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Original Research Article

Mean-variance relationships of leaf bilateral asymmetry for 35 species of plants and their implications

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ABSTRACT

Leaf bilateral asymmetry, an important indicator of leaves that tend to be affected by the above-ground architectural structure of plants and their environments (especially light), has been poorly studied. Taylor's power law (TPL) describes a power-law relationship between the mean and variance of a non-negative random variable, and its exponent has been demonstrated to reflect the degree of heterogeneity of the branch spatial arrangement of plants. In this study, we checked whether the mean-variance relationship of the absolute difference in area between the left and right sides of 11396 leaves from 35 species of plants within four families followed TPL. TPL was found to hold true for each species investigated here, and the estimated TPL exponents fell within a range of 1.5 to 2.0. At the family level, there were no any significant differences in the estimated exponents of TPL among the pooled data of Lauraceae, Oleaceae, and Bambusoideae, but those exponent values were significantly smaller than that of Magnoliaceae. We also pooled the data from the four families, and we found that there was a general rule for the mean-variance relationship for the bilateral asymmetry among the studied broad-leaved plants. Given the variety of leaf bilateral asymmetry among species, our results highlight the importance of plant aboveground architecture and the heterogeneity of leaves on different positions to a better understanding of leaf development mechanism and how it responds to the surrounding environment.

1. Introduction

A plant's leaves, providing the basis for carbon fixation, regulation of water and heat balance (Reich et al., 1992; Wright et al., 2004), play an important role in plant growth. Leaf morphological structure, including size and shape, is an important indicator of the photosynthetic capacity of plants, which results from long-term adaptation to the environment (Bar and

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Ori, 2014). Leaf development is extremely plastic and depends on genetic predisposition, leaf position, and environmental conditions. For example, leaf size is related to latitude: the average leaf size in the equatorial region is usually larger, and gradually decreases toward the two poles (Wright et al., 2017). In addition, smaller leaves are always found in drier and hotter places (Westoby et al., 2002). These reports reflect the adaptation of leaves to the regional differences in humidity, light, rainfall, and temperature. Studying the morphological characteristics of leaves can contribute to our understanding of how leaves interact within a particular environment in the long growing season across eco-evolutionary dynamics (Balduzzi et al., 2017).

Compared with other leaf traits (e.g, shape, specific leaf area, length, width, and thickness), the difference in leaf bilateral symmetry (asymmetry) has been less well studied (Wang et al., 2018). In fact, asymmetry is a prominent feature of leaves, which embodies the coordination of the left and right sides facing any gradients of environmental heterogeneity. The symmetry is mainly to satisfy the support function and plasticity coordination of the blade. Leaf shape and structure are evolving towards to maximizing the acquisition of resources, especially light, which largely affects photosynthesis (Niinemets et al., 2007). Because the height and location of the sun are constantly changing, and the light intensity and shading of the canopy leaves changing in consequence, the light available to leaf blades is also always changing. Generally speaking, under conditions with abundant rainfall, more light will result in bigger leaves and increased photosynthesis, but too much light can lead to photooxidation. This trade-off between maximizing photosynthesis and avoiding photooxidation determines blade size, shape, and to a large degree its asymmetry, which affects its ability to adapt to light on a finer scale (Bar and Ori, 2014). For a long time, the understanding of blade asymmetry stayed at the descriptive level, and a quantitative description of blade asymmetry has been poorly studied. Therefore, to quantify and compare the difference in the extent of leaf bilateral asymmetry among different plant families can help to better understand the difference in the adaptation strategies of leaves to different environments. Shi et al. (2018) provided a novel method for measuring leaf bilateral asymmetry by dividing a leaf into different subregions with equidistant strips. The mean of the percentages of the left to right side absolute area difference to the area sum of the left and right side of each subregion was proposed as a standardized index (SI) for measuring leaf bilateral asymmetry. The higher SI is, the greater the leaf bilateral asymmetry is. The standardized index has been demonstrated to be valid for many species (Shi et al., 2018; Yu et al., 2019a,b; Shi et al., 2020).

Taylor's power law (TPL) (Taylor, 1961) describes a power-law relationship between the mean and variance of a non-negative random variable, which has been widely verified in different study areas (Eisler et al., 2008; Fronczak and Fronczak, 2010; Shi et al., 2017, 2019). The scaling exponent of variance vs. mean, which is referred to as the exponent of TPL, has been a subject of controversy. Most empirical estimates of this exponent were found to fall within the 1 to 2 range, and debate has focused on whether the exponent of TPL results from a biological process, reflecting some unknown population characteristics or is just a statistical artifact (Cohen and Xu, 2015; Giometto et al., 2015; Xiao et al., 2015; Shi et al., 2016). Wang et al. (2018) first confirmed that TPL held true at the species level for leaf bilateral asymmetry measure using three groups of plants [10 naturally distributed geographical populations of *Parrotia subaequalis* (H.T. Chang) R.M. Hao et H.T. Wei, 10 species of Bambusoideae, and 10 species of Rosaceae]. For the pooled data at the group level or all the pooled data from the three groups, TPL still held true with a high goodness of fit. The estimated exponent of TPL for the pooled data in Wang et al. (2018) was 1.773 with a 95% confidence interval (1.760, 1.787). Shi and Liu (2019) also found that TPL for leaf bilateral asymmetry measure holds for the pooled data of two extant tulip trees (*Liriodendron chinense* and *Liriodendron tulipifera*) with their hybrid variety (*Liriodendron sino-americanum*), and obtained an estimate of the TPL exponent 1.777 with a 95% confidence interval (1.698, 1.857). It appears that there is a general power-law relationship between the mean and variance of leaf bilateral asymmetry measure among different broad-leaved plant groups. However, further evidence is still lacking. In addition, other leaf traits such as leaf roundness index and leaf surface area may influence the energy allocation inside a leaf, and may thus interact with leaf bilateral asymmetry. Leaf area is regarded as a reliable indicator of light interception and plant productivity (Gifford et al., 1984; Koester et al., 2014). However, due to the leaf overlap and curling that results from multilayered leaf arrangements, the effective leaf area is always significantly lower than the total leaf area (Weraduwagel et al., 2015). To reduce the overlap of leaves, plants have evolved various leaf shapes and aboveground architectures to enhance effective leaf area. In general, the lower leaf roundness index values correlate to larger effective leaf area, thus higher light efficiency (Niinemets et al., 2004). However, the relationship of these variables with leaf bilateral asymmetry is still poorly understood. Therefore, a combined study of leaf traits is needed to better understand the physiological and ecological processes of leaf growth.

In this study, we examined the leaf bilateral asymmetry of 35 species from four families (5 species of Lauraceae, 5 species of Magnoliaceae, 5 species of Oleaceae and 20 species of Bambusoideae [a subfamily of Poaceae]) to test whether the mean-variance relationships for leaf bilateral asymmetry measured at the species and family levels follow TPL, and to compare the range of variation in the estimated exponents of TPL. The relationships between the TPL exponent and the leaf roundness index, and between TPL's exponent and leaf surface area were also studied.

2. Materials and methods

2.1. Leaf collection and data acquisition

We chose a total of 35 plant species from four families, including 5 species each from the Lauraceae, Magnoliaceae, and Oleaceae families, and 20 species from the Bambusoideae subfamily. These families all have a long evolutionary history, and each family covers a large number of species. Thus, these families can be used to represent the typical broad-leaved plants to a large extent, and then the results may be applied to other broad-leaved plants. For each species, mature and healthy leaves were collected from plants growing in Nanjing, Jiangsu Province, China in 2018 and 2019. Two species of Magnoliaceae were collected from Nanjing Botanical Garden, Mem. Sun Yat-Sen, and the remaining 33 species were gathered from the Nanjing Forestry University campus. Table S1 shows the detailed scientific names, geographical locations of sampled plants, collection time, and the number of sampled leaves for each species.

Fresh leaves from plants were immediately put into transparent plastic self-sealing bags (28 cm × 20 cm) and placed in a foam box (29 × 16 × 18 cm) with ice to prevent leaf deformation and water loss, and leaves then were brought to the laboratory. We obtained scanned images of all the leaves at a 600-dpi resolution with a flatbed scanner (Aficio MP 7502; Ricoh, Tokyo, Japan), and then used the Matlab procedure developed by Shi et al. (2018) to extract the planar coordinates of leaves in batches. Based on the extracted planar coordinates of the leaf edge, we used the R (version 3.6.0; R Core Team, 2018) script developed by Shi et al. (2018) to divide a leaf into 1000 subregions as shown in Fig. 1. We then calculated leaf asymmetry as follows

$$AD_i = |L_i - R_i| \tag{1}$$

where L_i represents the left side surface area of the ith subregion ($i = 1, 2, \ldots, 1000$), i.e., the area of the intersection between the ith strip and the left side of the leaf; R_i represents the right side surface area of the ith subregion; and AD_i represents the absolute difference between L_i and R_i.

We used the leaf roundness index (RI) of Niinemets et al. (2004) to measure the extent of leaf shape complexity:

$$\mathrm{RI} = 4\pi A \,/\, P^2 \tag{2}$$

where A represents leaf area (cm^2), and P represents leaf perimeter (cm). These two variables need to be measured for each leaf using the method of Su et al. (2019). RI ranges from 0 to 1. If its value is closer to 1, the leaf is rounder; if its value is closer to 0, it indicates that the leaf largely deviates from a standard circle because of many teeth, dissections, and lobes on the leaf margin or a very small quotient of leaf width and length (i.e., a very narrow leaf shape).

2.2. Statistical analysis

We used Turkey's Honestly Significant Difference (HSD) (Hsu, 1996) to test whether there were significant differences in leaf roundness indices among the 35 species at a 0.05 significance level. We also calculated the coefficient of variation (= standard deviation/mean in %) for RI at the species and family levels.

The mean (M) and variance (V) of the absolute difference of the left to right side surface areas were calculated for each leaf. For a given species, there were N pairs of M and V for further calculation, where N represents the number of sampled leaves. According to Taylor's power law (TPL; Taylor, 1961), the mean-variance relationship is as follows:

$$V = \alpha M^{\beta} \tag{3}$$

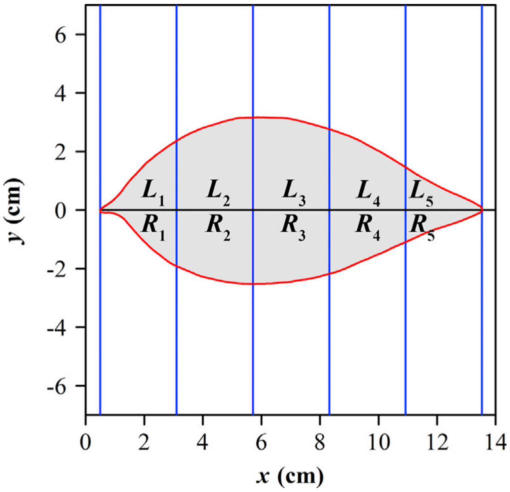

Fig. 1. Illustration for leaf bilateral asymmetry measure. There are five strips to conveniently show the calculation. However, in the actual calculation, 1000 strips were used.

To stabilize the variance of the response variable, we transformed TPL as follows:

$$\ln(V) = \gamma + \beta \ln(M) \tag{4}$$

where the log-transformed mean and variance were used in linear fit to estimate parameters β and γ for each species. In addition, in order to test for significant differences in the TPL exponents among species and families, the 95% confidence intervals (CIs) of the TPL exponents were calculated using the bootstrap percentile method based on 4000 simulations (Efron and Tibshirani, 1993; Sandhu et al., 2011). The coefficient of determination (i.e., r^2) was calculated to measure the goodness of fit of the linear equation. All statistical analyses and graphic production were performed with R software (version 3.6.1; R Core Team, 2018).

3. Results

There were significant differences in leaf shape complexity among the 35 species. *Magnolia denudata* Desr. had the greatest RI, and *Syringa oblata* var. *alba* Lindl. had the second greatest RI (Fig. 2a). *Pleioblastus chino* Makino had the smallest RI (Fig. 2b). Fig. 2 showed that the pooled leaves of Magnoliaceae were the roundest and had the smallest coefficient of variation in RI. Although the pooled leaves of Oleaceae were the second roundest, their coefficient of variation was the largest (Fig. 2c), which results from the largest interspecific difference among the five species within this family (Fig. 2a). All bamboo plants had lower RI values than those of the 15 trees sampled (Fig. 2a–c). At the species level, the interspecific difference in the RI's coefficient of variation for bamboo plants did not differ from species of Lauraceae or Oleaceae. However, those three families have larger coefficients of variation in RI than those of Magnoliaceae.

The mean-variance relationships of all the 35 species followed TPL because the lower bounds of the 95% confidence intervals for the estimated slopes were all greater than 1 (Fig. 3–4). The 35 coefficients of determination were all greater than 0.6. Considering that each sample size was greater than 250, the r^2 values (>0.6) showed a robust linear relationship in the data set. In fact, 30 out of the 35 r^2 values were found to be greater than 0.70. All species examined conformed to TPL. The estimated TPL exponents fell within a range of 1.5–2.0 (Figs. 3 and 4), and the 95% confidence intervals of the estimated slopes for 35 species fell within a range of 1.4–2.2 (Fig. 5b). The 35 intercepts were found to fall into a range of −4.5 to −0.5 (Figs. 3 and 4), and their corresponding 95% confidence intervals fell into a range of −5.0 to 0 (Fig. 5a).

At the family level, TPL also held for each pooled data set within a family. Among four families, the estimated TPL exponent of Magnoliaceae was equal to 1.918 (approximately 2), which was the largest; the estimated TPL exponents of the remaining three families had no significant differences, but the values were all lower than that of Magnoliaceae (Fig. 6). The pooled data for all four families' 11396 leaves conformed to TPL as well, with an estimated TPL exponent of 1.808 with a 95% confidence interval (1.797, 1.819) (Fig. 6e).

In addition, we did not find a correlation between the exponents of TPL and the mean or the coefficient of variation of leaf roundness index ($P > 0.05$), and there was also no correlation between the exponents of TPL and the mean or the extent of variation of leaf area ($P > 0.05$). Thus, there is no evidence to support that leaf shape and leaf size could significantly affect the scaling exponent of variance vs. mean for leaf bilateral asymmetry measure.

4. Discussion

4.1. Leaf bilateral symmetry and leaf development

Even though leaf functional traits (e.g., size, shape, specific leaf area, and thickness) are largely dependent on environmental factors and vary largely among species, most broad-leaved plants still have nearly symmetrical leaves. Our research shows the leaves of the four families all exhibited a certain level of bilateral asymmetry. The estimated 35 TPL exponents fell within the 1.5 to 2.0 range, which indicates a general feature of the mean-variance relationship for leaf bilateral asymmetry measure. That might reflect the importance of the response of the left and right sides of leaves to the efficiency of light intercept. This result is also closely related to the developmental process of leaves. Leaves are generated from shoot apical meristem (SAM) and initiate at the flanks of the SAM in a process involving the determination of proximodorsal and mediolateral axes of symmetry (Barton, 2010). Following initiation, leaf primordia differentiate in a highly flexible way that ultimately gives rise to the final leaf shape. The generation of the leaves and the formation of the symmetry are affected by the meristem of leaves, which first divides the cells and then enlarges the cells to form the leaves. This plasticity is manifested in a continuum of leaf shapes, ranging from very simple to highly complex. Leaf size is intrinsically affected by the number of cells and mean cell size in a leaf. The expansion of cells must balance the need for the physical support on the left and that on the right, which then results in the similar growth of both sides of a leaf.

The rate and extent of cylinder expansion are jointly regulated by genetic and environmental factors (Balduzzi et al., 2017), which may lead to imbalanced leaf growth and increased asymmetry. For example, light is the most important factor affecting leaf ontogeny. It has been demonstrated that in *Arabidopsis thaliana* (L.) Heynh., light signals could be received by phytochromes and cryptochromes of the leaf, leading to prolonged petioles and increased leaf area (Casal, 2012). A previous study has also shown that with increasing light intensity, important parameters of photosynthesis including leaf thickness, leaf

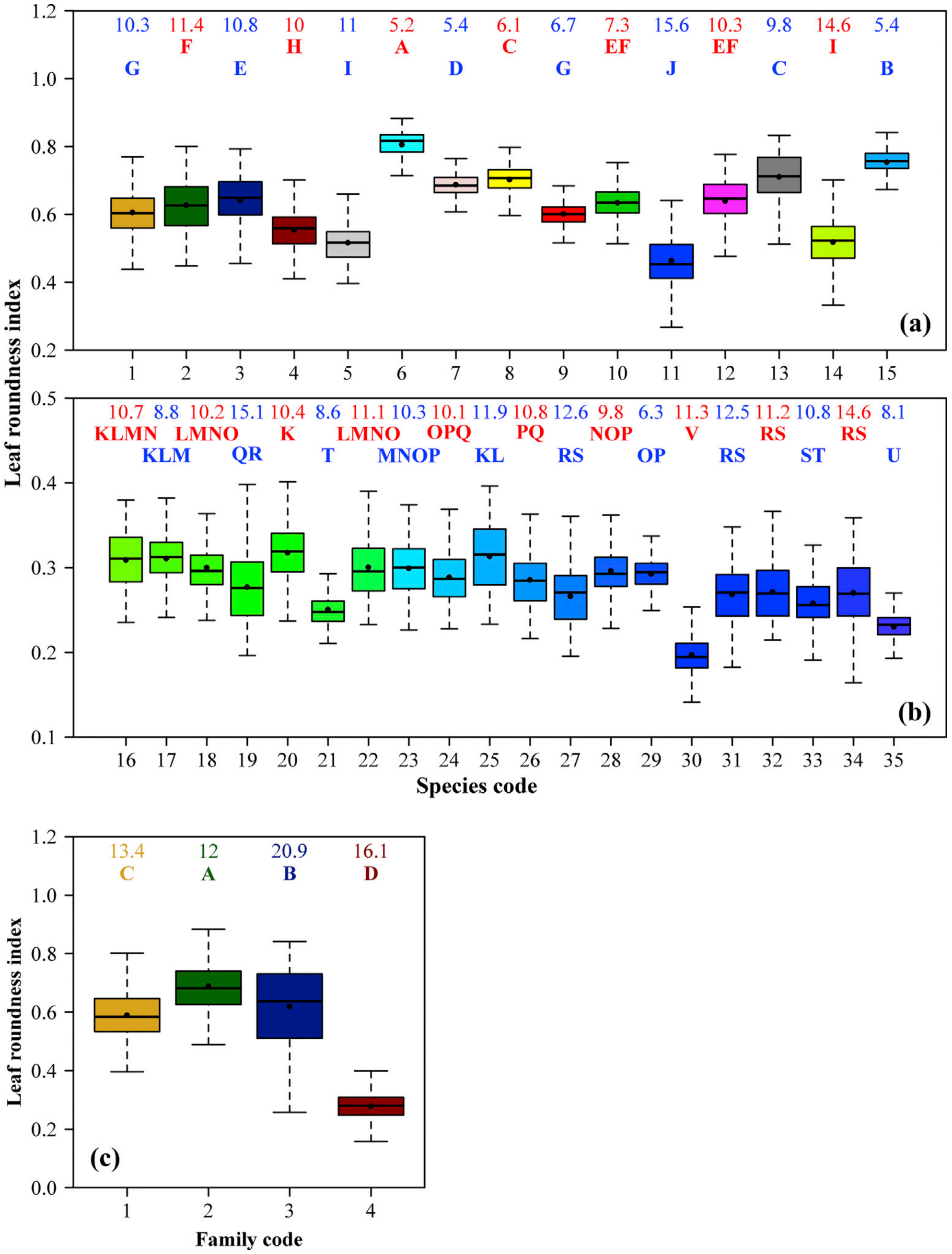

Fig. 2. Comparison of leaf roundness indices among 35 species: (a) the species in Lauraceae, Magnoliaceae and Oleaceae, (b) the species in Bambusoideae (Poaceae), and (c) comparison among four families based on the pooled data. The horizontal line in a box represents the median, and the point in the box represents the mean of leaf roundness indices; the numbers on the top of each panel represent the coefficients of variation; the upper letters are used to show the significance of the differences between any two species (or families). In panel c, family codes from 1 to 4 represent Lauraceae, Magnoliaceae, Oleaceae, and Bambusoideae, respectively.

density, and mesophyll cell surface area also increased (Chabot and Chabot, 1977), which in turn affects energy production and the fitness of the species. Therefore, the asymmetry is meant for maximizing the acquisition of resources, leaf growth, and carbon fixation. The interception of light by a plant depends on various factors, such as the light conditions of the surrounding environment, the location and distribution of leaves, and plant structure.

For the light conditions of the surrounding environment, the height of the sun, the temporal change of light intensity, and the light received by the leaves are always changing, so leaves are always evolving species-specific adaptation strategies. The higher heterogeneity of light leads to a larger variety of leaf asymmetry, which shows a more flexible adaptability of leaves to

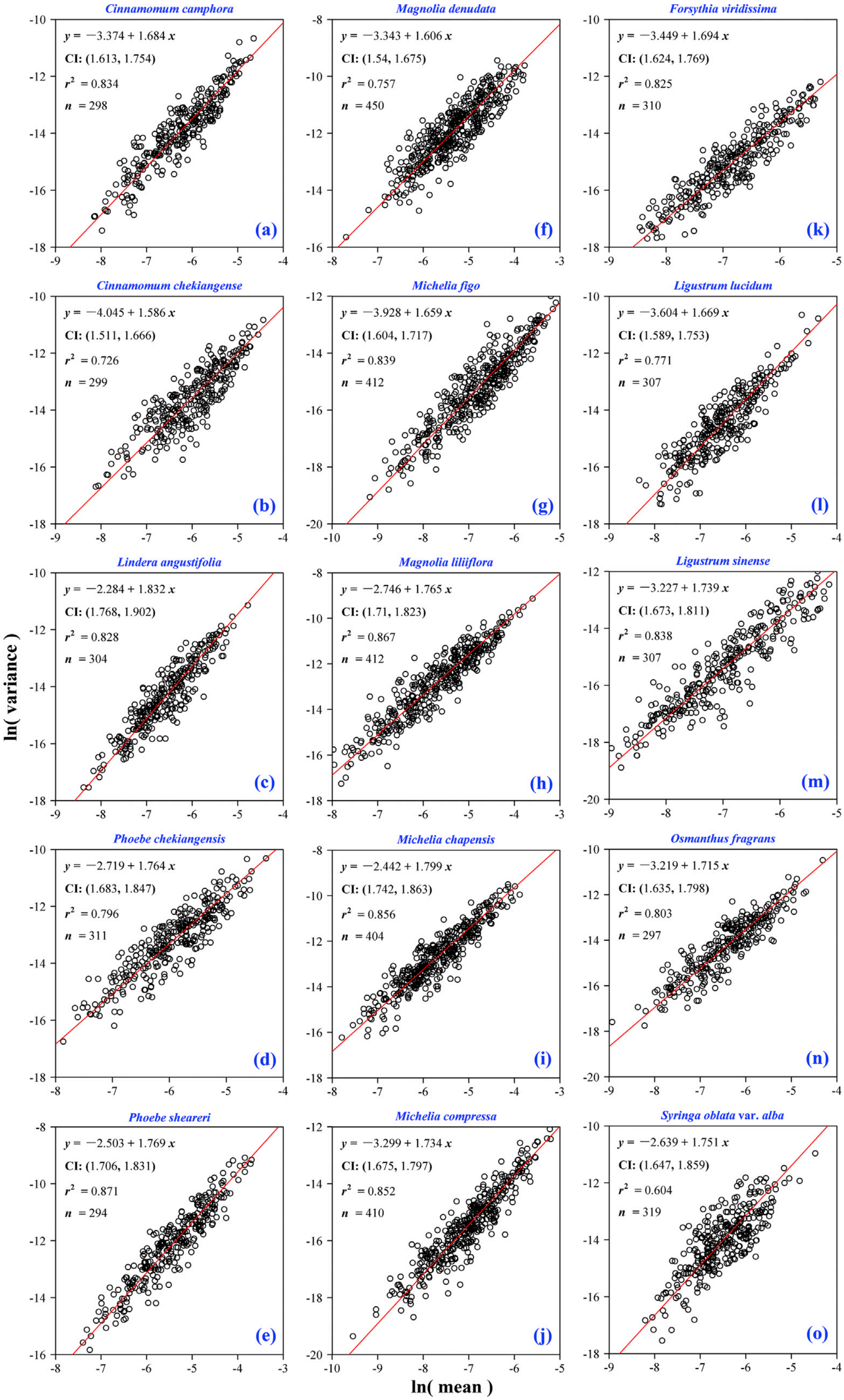

Fig. 3. Linear fit to Taylor's power law for three families of trees (Lauraceae, Magnoliaceae, and Oleaceae with five species for each family). On each panel, y represents ln(variance), and x represents ln(mean); CI represents the 95% confidence interval of the slope; r^2 is the coefficient of determination that is used to measure the goodness of fit; n is the sample size, i.e., the number of data points (leaves) for the linear fit. The small open circles represent the observations of ln(variance) vs. ln(mean); the straight line is the regression line.

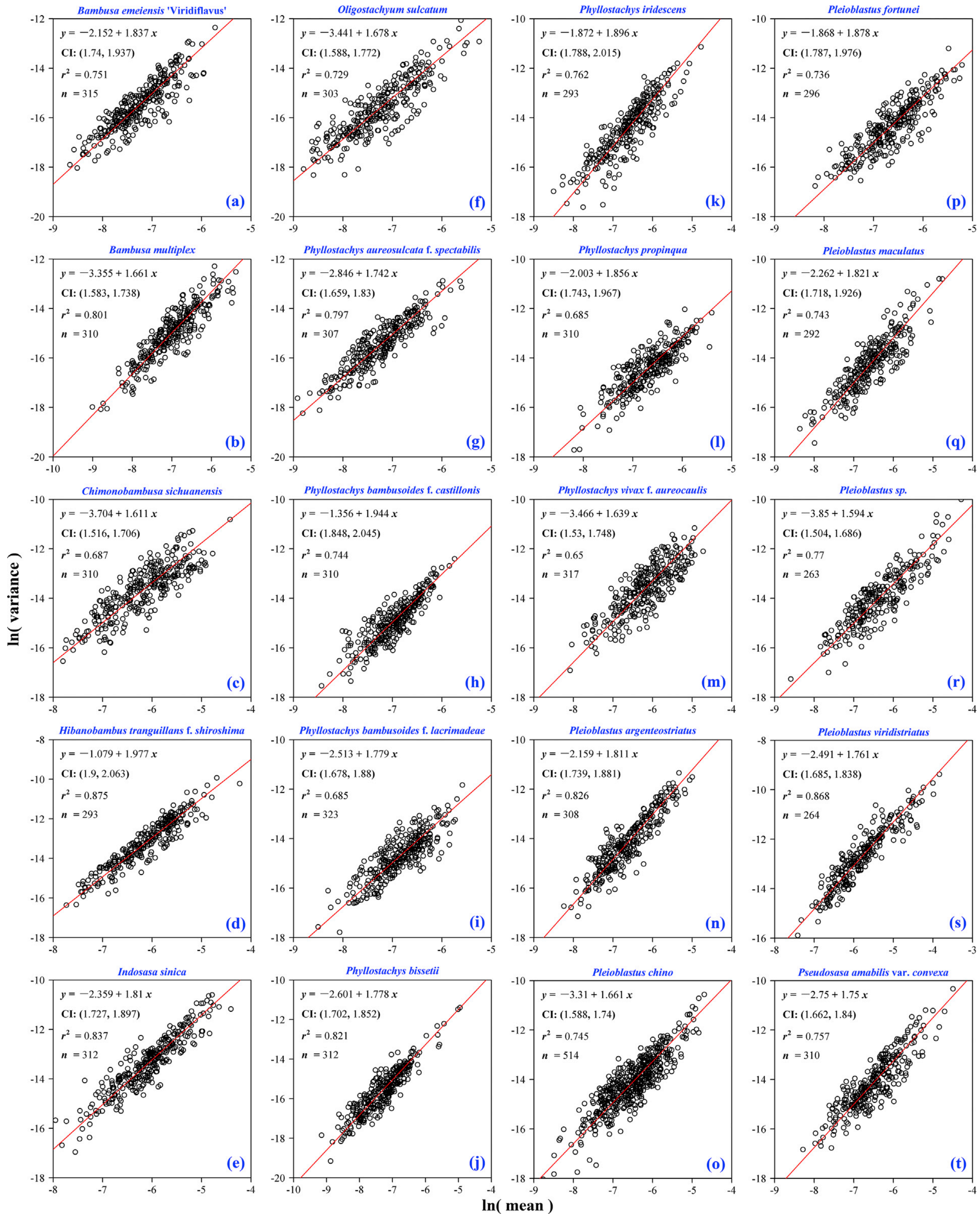

Fig. 4. Linear fit to Taylor's power law for 20 species of bamboos (Poaceae: Bambusoideae). On each panel, y represents ln(variance), and x represents ln(mean); CI represents the 95% confidence interval of the slope; r^2 is the coefficeint of determination that is used to measure the goodness of fit; n is the sample size, i.e., the number of data points (leaves) for the linear fit. The small open circles represent the observations of ln(variance) vs. ln(mean); the straight line is the regression line.

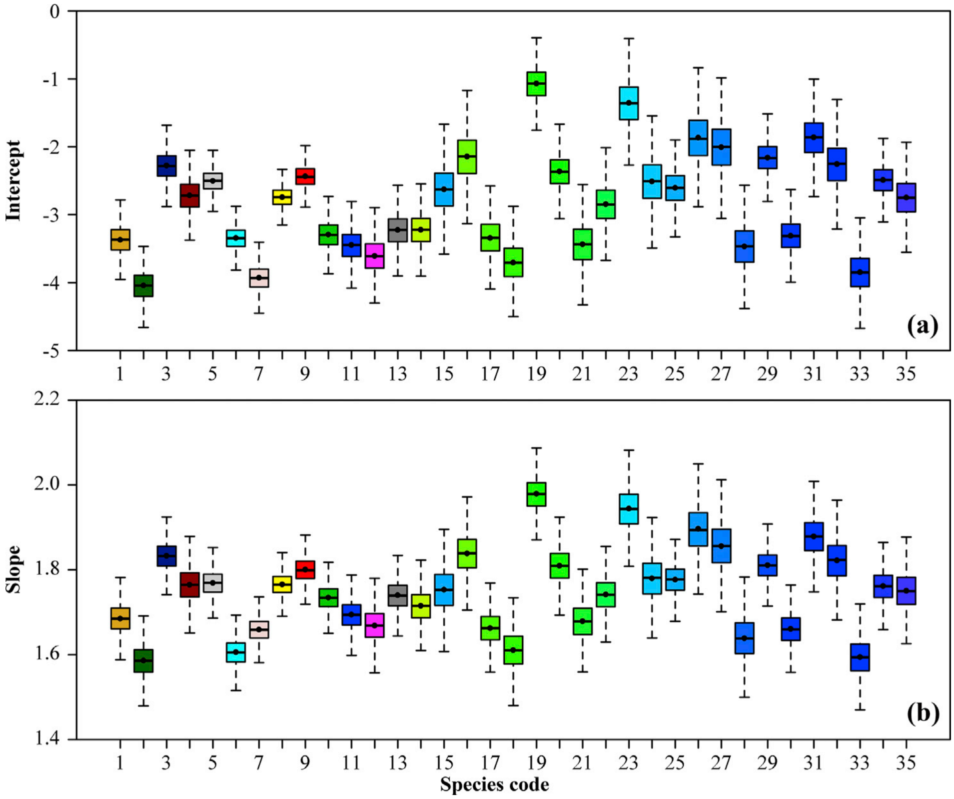

Fig. 5. Comparison among the 35 species in (a) the estimated intercepts, and (b) the estimated slopes in the linearized form of Taylor's power law. The horizontal line in a box represents the median, and the point in the box represents the mean of leaf roundness indices. There are 4000 bootstrapping replicates for each species.

the environment. Many studies have demonstrated that leaf area is normally distributed or skewed towards the top of the crown in many conifer species (Lange et al., 2012) and broad-leaved species (Medhurst and Beadle, 2001). For example, the leaves in upper canopy can receive more light than those in shaded lower canopy, which renders plants to invest more energy to the top canopy for promoting total leaf area and photosynthetic efficiency (Vialet-Chabrand et al., 2017). In the above-ground architecture, branch length and angle are important indicators of competitive ability to capture light (Barthelemy and Caraglio, 2007). For example, long and horizontally extended branches would be shaded by neighboring crowns while upright branches could get more chances to receive light (Sumida et al., 2002).

In this study, the estimated exponent of TPL for the pooled data of the Magnoliaceae plants was the greatest among the four families, indicating that the Magnoliaceae plants may have a more irregular aboveground architecture for branches and leaves and consequently exhibit a greater heterogeneity for light intercept than other plants investigated here. Meanwhile, the RI value of Magnoliaceae was also significantly greater than each of the RI values of the other three families, indicating that the effective leaf area may be the smallest. It suggests that there exists a trade-off between leaf asymmetry and roundness, which further implies that a small value of the effective leaf area has been compensated by a great extent of the plasticity in adjusting leaf asymmetry to maximum light capture and photosynthetic efficiency. However, in this study, the correlations between the TPL exponent and leaf shape, and between the TPL exponent and leaf area are not significant. TPL in leaf bilateral asymmetry is closely correlated to the energy distribution in leaves (Wang et al., 2018). Leaf biomass is a product of leaf area, thickness and density. Studies have demonstrated that leaf thickness is more important than the leaf area for predicting leaf biomass based on a leaf growth model (Weraduwagel et al., 2015). However, in our study, leaf thickness has been neglected, which probably leads to such this insignificance for a correlation between the TPL exponent and leaf area (also leaf shape). Another reason may be due to the limitation of the sample size (i.e., the number of the studied species). Therefore, more leaf traits especially leaf thickness and more species within the same taxon deserves a further investigation to better understand leaf growth mechanisms in future studies.

4.2. The exponent of Taylor's power law

There is a debate on whether the TPL exponent is a pure statistical artifact or is a result of a context-dependence process (Giometto et al., 2015, and references therein). Cohen and Xu (2015) found that the mean-variance relationship could be

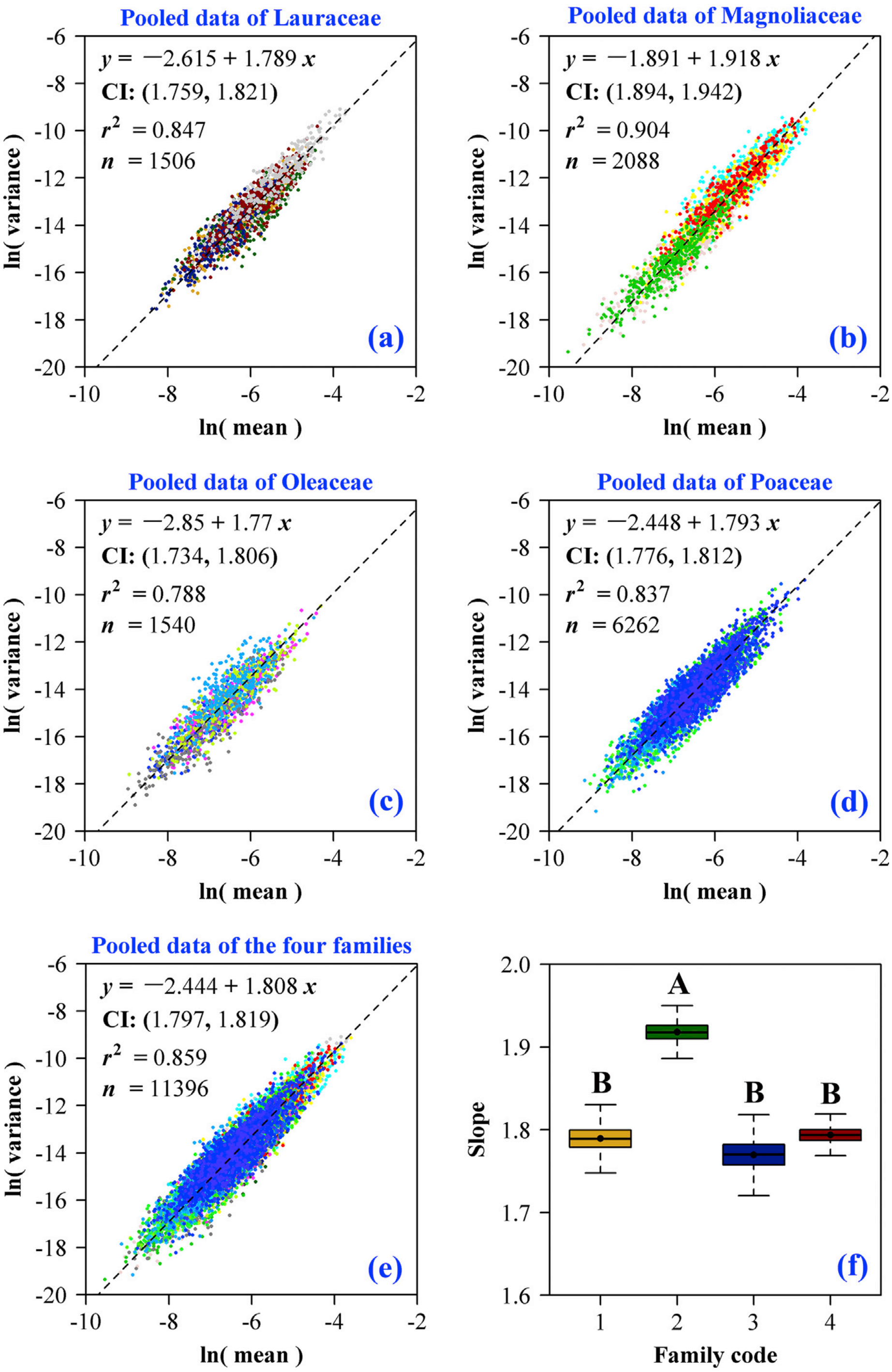

Fig. 6. Linear fit to Taylor's power law for the pooled data at the family level. On panels a–e, y represents ln(variance), and x represents ln(mean); CI represents the 95% confidence interval of the slope; r^2 is the coefficeint of determination that is used to measure the goodness of fit; n is the sample size, i.e., the number of data points (leaves) for the linear fit. The small open circles represent the observations of ln(variance) vs. ln(mean); the straight line is the regression line. Panel f compares the significance of the differences between any two families in the estimated slopes, i.e., the TPL exponents. The letters on the top of boxes show the significance.

generated from any skewed distribution, and the TPL exponent is proportional to the skewness of the distribution. Giometto et al. (2015) proposed a generalized TPL that describes a scaling of two raw moments for the realizations of a non-negative random variable, and they found that the exponent of the generalized TPL is approximately equal to the quotient of the cumulants of the two raw moments. They concluded that the exponent of the conventional TPL should approximate 2 since the generalized TPL predicted an exponent 2 for the scaling of the second moment vs. the first moment. However, according to our recent study, the conclusion of Giometto et al. (2015) is limited to some special cases where the empirical estimate of the TPL exponent is equal or very approximate to 2 itself. For two cumulants with a large numerical difference, the exponent of the generalized TPL can deviate from the quotient of the two cumulants largely. Thus, their study still cannot disprove the hypothesis of TPL is a result of a context-dependent process. Wang et al. (2018) stated that TPL's exponent of leaf bilateral asymmetry measurements might be linked to the influence of the aboveground architectural structure of plants on the light interception. Because of the spatial heterogeneity of leaf distribution in a plant, two sides of a leaf in both sun and the shade might tend to differ in size. The side that receives more light might be bigger than the side in shade to take better advantage of the available light (Yu et al., 2019a). Cheng et al. (2017) demonstrated that the TPL relationship of a higher physical measurement dimension for a bamboo's internode measure would have better goodness of fit than that of a lower physical dimension. Shi et al. (2019) found leaf dry mass can have a better TPL relationship than leaf fresh mass, surface area, and leaf length based on 101 bamboo taxa. The study of Giometto et al. (2015) also demonstrates that the goodness of fit for the generalized TPL is closely related to the measurement dimension (i.e., the numerical value of the quotient of two cumulants). A sufficiently high physical measurement dimension could have a perfect linear fit for TPL. However, the TPL exponent appears not to be purely a statistical artifact. Although TPL holds true for the pooled data (Fig. 6e), the estimated TPL exponent vary largely across species. We believe that despite the interspecific difference of energy allocations to two sides of a leaf, broad-leaved plants might have a general power law for the mean-variance relationship. Thus, we pooled more data than were reported by Wang et al. (2018) and Shi et al. (2020). Fig. 7 shows TPL of the bilateral asymmetry measure for 24435 leaves. The estimated TPL exponent equals 1.893 with a 95% confidence interval (1.883, 1.903), which does not overlap with that reported using the four families above (Fig. 6e). This means that with more data from more plant taxa a general TPL relationship for leaf bilateral asymmetry measurements could be discovered in spite of the differences in the numerical values of the TPL exponent resulting from the intraspecific, interspecific, and inter-taxon differences. Whether these differences could be used to check the evolutionary or ecological links for different plant taxa deserves further investigation.

In the present study, 20 bamboo species have been growing naturally in Nanjing Forestry University campus for at least 10 years, and there is very little human disturbance (including irrigation and logging) to these plants. Thus, the growth is almost wild. For the three families of trees, the growth is really not the same as in the wild. However, Wang et al. (2018) demonstrated that the estimates of the TPL exponent for the leaves of ten wild geographical populations of *Parrotia subaequalis* (H. T. Chang) R. M. Hao et H. T. Wei, which were collected from the natural distributed regions in Eastern China, also range from 1.5 to 2, which was similar to the numerical values of those leaves sampled from the cultivated plants. In addition, for the investigated three families of trees, most trees (especially the species of the Magnoliaceae family) have a large number of leaves. The response of leaf morphological structures to light and the difference of light capture between different layers of the canopy should be similar to those of wild trees. However, the interspecific and intraspecific competition (especially that for light) in forest communities can influence leaf shape and size. Whether such an influence of the competition can be reflected by the numerical value of the TPL exponent also merits a further study.

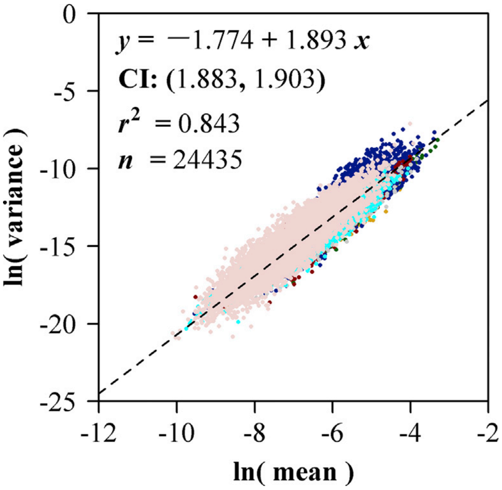

Fig. 7. Linear fit to Taylor's power law for the pooled data for 65 species. y represents ln(variance), and x represents ln(mean); CI represents the 95% confidence interval of the slope; r^2 is the coefficeint of determination that is used to measure the goodness of fit; n is the sample size, i.e., the number of data points (leaves) for the linear fit. The small open circles represent the observations of ln(variance) vs. ln(mean); the straight line is the regression line. Except from the current four families, we added the leaves of 10 geographical populations of *Parrotia subaequalis* (H.T. Chang) R.M. Hao et H.T. Wei (Wang et al., 2018), 12 species of Rosaceae (Yu et al., 2019a), and 15 species of vines (Shi et al., 2020).

For a mirror-symmetrical leaf shape, the concept of fluctuating asymmetry was adopted in the robust estimation of landmark differences. It reveals only minor directional asymmetries, but high variability in all dimensions, related to the various possible leaf deformations in the three-dimensional space, such as rolling, folding or tilting (Schmidt and Kahlen, 2018). This general "constraint" at the level of light-harvesting, which may reflect the ancestral traits (metabolic, anatomical, and morphological) shared by diverse non-vascular plants and all tracheophytes, helps to explain why total annual growth fails to keep pace with increases in body mass across plant species.

Leaf morphology, especially leaf bilateral asymmetry, embodies the plasticity of leaf development in response to the internal (genes, hormone) and external (environmental) cues. However, little attention has been paid to the comparison of the intra-and inter-specific differences in leaf bilateral asymmetry. In this study, we used 35 species belonging to the families of Lauraceae, Magnoliaceae, Oleaceae, and Bambusoideae to examine whether the mean-variance relationships for leaf bilateral asymmetry measure follow a power law function (i.e., Taylor's power law; TPL). TPL has been verified at the species level and the family level. The estimated exponents of TPL for the 35 species fell within a range of 1.5–2.0, which was in accordance with the 1 to 2 range most observed. Except a somewhat greater estimate of the TPL exponent for Magnoliaceae, the estimated TPL exponents for the remaining three families showed no significant differences. The pooled data of the four families still followed TPL, with an estimated TPL exponent of 1.808, which shows that the variation in leaf bilateral asymmetry measure is a general power function of its mean and that further implies that broad-leaved plants have the same scaling limitation on bilateral growth of leaves, suggesting that the variability in the left to right side area difference does not keep pace with its mean. In our study, the numerical value of the TPL exponent of for the Magnoliaceae species was the greatest among the studied four families, indicating that the Magnoliaceae plants may have a more irregular aboveground architecture for outlines (especially the clustering of branches) and exhibit a greater heterogeneity of light intercept for leaves. Thus, the plants with a larger deviation from a perfect bilateral symmetry have more heterogeneous leaf shapes, and the deviation is likely to reflect the influence of light heterogeneity casued by the spatial clustering arrangement of branches on the shapes of the leaves on different positions of plants.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01152.

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