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Leaf area-length allometry and its implications in leaf-shape evolution

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Abstract:	According to Thompson's principle of similarity, the area of an object should be proportional to its length squared. However, leaf area-length data of some plants have been demonstrated not to follow the principle of similarity. We explore the reasons why the leaf area-length allometry deviates from the principle of similarity and also examine whether there is a general model describing the relationship among leaf area, width and length. More than 11,800 leaves from the six classes of woody and herbaceous plants were sampled to check the leaf area-length allometry. Six mathematical models were compared based on root-mean-square error as the measure of goodness-of-fit. The best supported model described a proportional relationship between leaf area and the product of leaf width and length (i.e., the Montgomery model). We found that the extent to which the leaf area-length allometry deviates from the principle of similarity depends upon the variation of the ratio of leaf width to length. Estimates of the parameter of the Montgomery model ranged between 1/2 and π/4 for the six classes of plants. This is a narrower range than imposed by the limits 1/2 (for a triangular leaf with leaf length as its height and leaf width as its base) to π/4 (for an elliptical leaf with leaf length as its major axis and leaf width as its minor axis). The narrow range in practice implies an evolutionary stability for the leaf area of large-leaved plants despite the fact that leaf shapes of these plants are rather different.

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Leaf area-length allometry and its implications in leaf-shape evolution

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Abstract According to Thompson's principle of similarity, the area of an object should be proportional to its length squared. However, leaf area-length data of some plants have been demonstrated not to follow the principle of similarity. We explore the reasons why the leaf area-length allometry deviates from the principle of similarity and also examine whether there is a general model describing the relationship among leaf area, width and length. More than 11,800 leaves from the six classes of woody and herbaceous plants were sampled to check the leaf area-length allometry. Six mathematical models were compared based on root-mean-square error as the measure of goodness-of-fit. The best supported model described a proportional relationship between leaf area and the product of leaf width and length (i.e., the Montgomery model). We found that the extent to which the leaf area-length allometry deviates from the principle of similarity depends upon the variation of the ratio of leaf width to length. Estimates of the parameter of the Montgomery model ranged between 1/2 and $\pi/4$ for the six classes of plants. This is a narrower range than imposed by the limits 1/2 (for a triangular leaf with leaf length as its height and leaf width as its base) to $\pi/4$ (for an elliptical leaf with leaf length as its major axis and leaf width as its minor axis). The narrow range in practice implies an evolutionary stability for the leaf area of large-leaved plants despite the fact that leaf shapes of these plants are rather different.

Keywords Allometry · Montgomery model · Leaf area · Leaf dimension · Thompson's principle of similarity

Key message **Leaf area is proportional to the product of leaf length and width both for herbaceous and woody plants. The coefficient of proportionality ranges from 1/2 to $\pi/4$ for investigated species.**

Introduction

Thompson (1917) stated that the area of an object is proportional to the square of its length (the area-length allometry), and its weight is proportional to its area to the power 3/2 if the density of the object is regular (the weight-area allometry). These two proportionalities were referred to as the principle of similarity. Although the actual estimates for the power of the area-length allometry and that of the weight-area allometry in biology are not exactly equal to 2 and 3/2, estimates from biological data often approximates those values. For instance, O'Shea et al. (2006) studied the allometric relationship between the surface and the length and that between the surface and the weight of six species of fish. The estimates of the exponent of the first allometry ranged from 1.88 to 2.22, and the estimates of the exponent of the second allometry ranged from 1.54 to 1.69.

These allometric relationships are also of special importance for leaves. Leaves, as important photosynthetic organs of plants, have been in the core of physiological and functional ecology and knowledge about the scaling of leaf dimension is important to understand ecosystem processes and plant life strategies (Westoby 1998; Wright et al. 2004). The leaf weight-area allometry has been reported for many leaves (Milla and Reich 2007; Li et al. 2008; Sun et al. 2017; Lin et al. 2018). However, estimates of the exponent of the leaf weight-area allometry are usually lower than 3/2. For instance, Milla and Reich (2007) explored the range of the estimates of the exponent of the leaf weight-area allometry using a large dataset of over 150 species. The mean estimated over all species they obtained was 1.10 with 95% confidence intervals ranging from 1.08 to 1.13 (the use of confidence intervals is of special importance in this regard, as they indicate the range of intraspecific variation of the exponent of the leaf weight allometry). Lin et al. (2018) studied the leaf weight-area allometry for bamboo species and found that the estimate of the exponent for the pooled data was 1.15 with a 95% confidence interval of 1.14 to 1.15. However, the exponent reported by both studies was far from the 1.5 calculated for the principle of similarity (Thompson 1917). Lin et al. (2018) found that leaf weight was approximately proportional to leaf area to the power 9/8. This indicates that leaf density decreases as leaf thickness increases. Other studies have verified that leaf thickness can affect the leaf weight-area allometry (Witkowski and Lamont 1991; Yano and Terashima 2004; Griffith et al. 2016). In comparison with leaf weight-area allometry, area-length allometry has been little studied, although there would be many advantages, such as an expression in dimensional terms of length and width of a leaf, which would be easy to measure in the field.

Many studies have provided parametric models to describe leaf shapes of some plants, especially for the plant family Poaceae. These models can be used to calculate leaf area. Dornbusch et al. (2011) proposed a general parameter model to depict the leaf shapes of wheat, barley and maize. Gielis (2003) proposed a superformula that

can be used to describe the shapes of many abiotic and biotic shapes, which has been simplified to fit to leaf dimensions. The simplified Gielis equation (SGE) has only two parameters of which one is related to leaf length, and another is related to the ratio of leaf width to length. Shi et al. (2015b) and Lin et al. (2016) used this simplified version to fit the leaf shapes of 46 bamboo species and found that the model generally performed well for the very similar leaf shapes of bamboos. Here, the corresponding estimates of the second parameter (related to the ratio of leaf width to length) only varied in a narrow range. Shi et al. (2018a) found that the simplified Gielis equation is also applicable to the leaves of other plants such as *Aucuba japonica* var. *variegata* Dombrain, *Chimonanthus praecox* (L.) Link, *Parrotia subaequalis* (H. T. Chang) R. M. Hao & H. T. Wei, *Phoebe sheareri* (Hemsl.) Gamble and *Pittosporum tobira* (Thunberg) W. T. Aiton. Leaf area for these species can be reliably estimated based on this simplified equation. However, these methods are only suitable for describing particular leaf shapes. Montgomery (1911) put forward a leaf-area formula for corn: leaf area (A) = a_1 × leaf length (L) × leaf width (W), where a_1 is a constant to be fitted; leaf length is defined as the distance from leaf apex to leaf base; leaf width is defined as the maximum length of the segments perpendicular to the straight line passing through leaf apex and leaf base (Shi et al. 2018b). This model has been also demonstrated to be powerful in calculating leaf area for other plants such as castor, cotton, rice and sorghum (Jani and Misra 1966; Palaniswamy and Gomez 1974 and references therein). The Montgomery model has been widely applied to calculate the area of herbaceous plants, especially for crops. However, there are only a few studies that have reported its validity for calculating the leaf area of woody plants. For instance, Verwijst and Wen (1996) used the Montgomery model to fit data on leaf area, length and width of basket willow (*Salix viminalis* L.). In addition, they also compared this model with other models using leaf area as the response variable with leaf length (or leaf width) as the explanatory variable. They found that the Montgomery model was the best among these models. Since then no further studies have focused on the leaves of woody plants. In addition, the previous studies all used a single species without using extra species to test the model's validity. If the Montgomery model holds for most broad-leaved plants, then whether or not Thompson's principle of similarity holds in these plants depends upon the relationship between leaf width and length. The principle of similarity will hold if there is a proportional relationship between leaf width and length; if so, the estimate of the exponent for the leaf area-length allometry will equal 2. Otherwise the exponent will deviate from 2. Furthermore, the leaf weight-area allometry is affected in a similar way.

In this contribution, we used six plant morphological groups to test the validity of the Montgomery model: 10 populations of *Parrotia subaequalis* (H. T. Chang) R. M. Hao & H. T. Wei, 5 species of Lauraceae, 2 species of tulip trees with their hybrid, 5 species of Oleaceae, 12 species of Bambusoideae, and 12 species of Rosaceae.

In addition, we also examined a set of other leaf-area allometric models to test whether the Montgomery model was the best-performing for fitting the observed data.

Materials and methods

Collection information

The leaves of 10 populations of *P. subaequalis* (with 150 leaves or so for each population) were collected in Eastern China from July to September, 2016 (see Table S1 in Electronic Supplementary Material); the leaves of 5 species of Lauraceae (each species≥ 300 leaves) were collected in the Nanjing Forestry University campus, China from late August to early October, 2018 (see Table S2 in Electronic Supplementary Material); the leaves of American tulip trees (*Liriodendron chinense* (Hemsl.) Sarg.) and Chinese tulip trees (*Liriodendron tulipifera* Linn.) with their hybrid (*Liriodendron chinense* × *tulipifera* P. Z. Ye) (each species ≥ 170 leaves) were collected in Nanjing, China on 11 October, 2017 (see Table S3 in Electronic Supplementary Material); the leaves of 5 species of Oleaceae (each species≥ 300 leaves) were collected in the Nanjing Forestry University campus, China from late August to early October, 2018 (see Table S4 in Electronic Supplementary Material); the leaves of 12 bamboo species (with 100−500 leaves for each species) were collected in the Nanjing Forestry University campus, China from early July of 2014 to early July of 2018 (see Table S5 in Electronic Supplementary Material); and the leaves of 12 species of Rosaceae (each species≥ 300 leaves) were collected in the Nanjing Forestry University campus, China from late April to early May, 2018 (see Table S6 in Electronic Supplementary Material).

Data acquisition

Leaves were scanned to bitmap format (used scanner: Aficio MP 7502; Rocoh, Japan). The image resolution was 400 dpi. Then, we used Matlab (version ≥ 2009a) procedures proposed by Shi et al. (2015a, 2018a) to extract the leaf profile data. The R procedures proposed by Shi et al. (2018a) were then used to adjust the leaf profile data and calculate leaf area, length and width.

Statistical analysis

We used six models to fit leaf area data (Table 1). For simplification, we will refer to the parameter of model 1 as the Montgomery parameter below. We used the log-log method to stabilize the variance of the observations of leaf area in data fitting (Table 1) because many biological measures exhibited a power-function relationship between the variance and mean that implies heteroscedasticity (Shi et al. 2017). Model fitting was carried out using least-

squares linear regression to estimate the parameters. For models 2−4, we calculated the 95% and 99.7% confidence intervals of the slope (which correspond to the estimate of the slope ±1.96 times its standard deviation and to the estimate of the slope ±3 times its standard deviation, respectively). By this means, we tested whether model 2 could be simplified to model 1. Our criterion was that if the 99.7% confidence intervals of the slope of model 2 for most data sets included 1, then that indicated that model 2 could be replaced by model 1. Here, 95% confidence intervals also served as a reference.

To measure the goodness of fit of the linear regression, we took the root-mean-square error (RMSE):

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}\left(y_i - \hat{y}_i\right)^2}{n}} \quad (1)$$

Here, y represents the natural logarithm of leaf area; the subscript i represents the i-th leaf; and the circumflex on the y represents the predicted value using a model.

After finding the best model, we used the pooled data for every class of plants to test whether there were significant differences in the estimates of a particular parameter of interest among the six classes. For this purpose, we used the bootstrap percentile method (Efron and Tibshirani 1993; Sandhu et al. 2011) to test the significance of the differences among the parameter estimates. For example, if model 1 was the best, we were concerned with whether the estimates of the constant a_1 (Table 1) for six classes of plants were significantly different.

Statistical software

Matlab (version R2009a) was used to extract leaf profile data from the scanned bitmap image (Shi et al., 2015a, 2018a). R (version 3.2.2; R Core Team 2015) was used to carry out the statistical calculations. Packages ´spatstat´ (version 1.43-0.025) and ´splancs´ (version 0.4-19) were used to adjust leaf profile data and to calculate leaf area.

Results

Model 2 consistently has the lowest RMSE, with the RMSE of model 1 (namely the Montgomery model) being slightly higher than that of model 2 (Table S7 in Electronic Supplementary Material shows the RMSEs of the 37 data sets). Models 3−6 always have a worse goodness of fit than models 1−2. Figs. 1−6 exhibit the fitted results using model 1. The estimates of the parameters of models 1−6 are listed in Table S8 in Electronic Supplementary Material. The estimates of the parameter of model 1 among 47 data sets ranged from −0.56 to −0.30, and the corresponding values of the antilogarithm (namely the Montgomery parameter) varied in a small range from 0.57 to 0.74. The 95% confidence intervals of these estimates all fall into the range (0.5, π/4) (Figs. 1−4). Although

158 model 2 had a slightly better goodness of fit than model 1, the estimates of the slope of model 2 did not substantially
159 deviate from unity. There were 21 among 47 data sets whose 99.7% confidence intervals (i.e., the estimate ±3
160 standard deviations) included 1. In the remaining 26 data sets, the lower bounds (or upper bounds) of the 99.7%
161 confidence intervals differed from unity by less than 0.05 except for data sets 30 (*Indosasa sinica* C. D. Chu et C.
162 S. Chao) and 41 (*Kerria japonica* (L.) DC.). It is worth pointing out that the leaves of *K. japonica* are more
163 bilaterally asymmetric than those of the other species of Rosaceae investigated. That means that the scanned leaf
164 length, defined as the distance in a straight line from leaf apex to leaf base, will not closely correspond to the
165 position of the leaf's main vein.

166 Fig. 7 shows the fitted results for the pooled leaf-area data for each of the six classes of plant. The goodness
167 of fit is high, with the correlation coefficient exceeding 0.98 for each of the six classes. There were significant
168 differences in the estimates of the Montgomery parameter among the six classes. The estimates of the Montgomery
169 parameter for the pooled data of *Liriodendron* and Bambusoideae were significantly higher than those of other
170 classes (Fig. 8). Overall, there was a significant difference in the estimate of the Montgomery parameter between
171 any two classes of plants.

172

173 ## Discussion

174 **Influence of the relationship between leaf length and width on the principle of similarity**

175 The Montgomery model has been confirmed to be valid in predicting the leaf areas of many crops (Jani and Misra
176 1966; Palaniswamy and Gomez 1974 and references therein), but it has not been used to analyze leaf area-length
177 allometry. If leaf area is proportional to the product of leaf length and width, then it follows that the relationship
178 between leaf length and width will affect the leaf area-length allometry. If leaf length is proportional to leaf width,
179 leaf area will be proportional to leaf length squared (or leaf width squared). This will be in line with the principle
180 of similarity. To test this hypothesis, we calculated the coefficients of variation (CVs) in the ratio of leaf width to
181 length for each species (Fig. 9a) and checked whether the CVs were related to the RMSE values of model 5. Indeed,
182 the correlation coefficient of model 5 reached 0.85 ($P < 0.01$), thereby supporting the principle of similarity (Fig.
183 9b). This means that the scaling stability of leaf shape, which denotes that the ratio of leaf width to length for
184 leaves of different sizes is approximately constant, will determine whether there is a good proportional relationship
185 between leaf area and leaf length squared. The simplified Gielis equation (SGE) has been demonstrated to be a
186 good approach to describe the leaf shapes of bamboos (Gielis 2003; Shi et al. 2015b; Lin et al. 2016, 2018). Lin et
187 al. (2018) demonstrated mathematically that leaf area is proportional to leaf length squared on the condition that

188 the leaf-shape parameters for leaves have a small variation. The leaf shapes of bamboos were very similar to each
189 other, so that model 5 fits their data well. However, although the ratios of leaf width to length of bamboos are
190 significantly lower than those of the other five groups of plants (Fig. 7A), the CVs of the ratios of leaf width to
191 length were not significantly lower than those of the others. Surprisingly, despite the complex leaf shapes of tulip
192 trees, their CV of the ratios of leaf width to length were very low, lower than for the other plants investigated.
193 American and Chinese tulip trees exhibit a certain difference in leaf shape, even though both species are closely
194 related (Fang, 1994). For example, the angle formed by two lobes on the leaf top of American tulip trees is usually
195 smaller than that of leaves of Chinese tulip trees. However, Shi and Liu (2018) reported that there was no
196 significant difference in leaf bilateral symmetry measures among the two species and their hybrid. Thus, we had
197 grounds for believing that the leaves of tulip trees might exhibit a type of uniform isotropic growth in different
198 directions from the leaf margin (Coen et al. 2004). This should be a major cause of the small variation in the ratios
199 of leaf width to length. Verwijst and Wen (1996) studied the leaf allometry of basket willow (*S. viminalis*) and
200 found that the ratio of leaf width to length decreased with increasing leaf length. We calculated the correlation
201 coefficients of leaf length and the *W/L* ratio for 47 data sets and found that most data sets exhibited a negative
202 correlation. Additionally, we calculated the estimate of the slope of the linear equation between the *W/L* ratio and
203 leaf length for each data set, and the slopes associated with the significant correlations were larger than −1. This
204 indicated that the significance of the correlation did not result from the negative relationship between $1/L$ and L
205 itself (see Table S9 in Electronic Supplementary Material). The correlations of 32 of the 47 data sets were
206 significant, indicating that the *W/L* ratio decreased with increasing leaf size. However, the correlations for the
207 remaining 15 data sets were insignificant as all have lower CV values. This meant that the *W/L* ratios representing
208 leaf shapes for these plants remained stable among different individual leaves.
209
210 **About two kinds of special leaf shapes**
211 All estimates for the Montgomery parameter range from 0.5 to $\pi/4$ (Figs. 1−6). That is in line with previous
212 findings on the Montgomery parameter of other species (Jani and Misra 1966; Palaniswamy and Gomez 1974;
213 Verwijst and Wen 1996; de Swart et al. 2004). However, challenges remain how to discern the factors that most
214 strongly influence the estimate of the Montgomery parameter. That could, however, be solved by the comparison
215 of two major leaf shape functions, the SGE (Shi et al. 2015b) and the area formula of a triangle (i.e., area =
216 1/2×base×height). The SGE performed well in fitting the leaf shapes of some plants. It is usually given in the polar
217 coordinate form:

$$r = \frac{l}{\left(\cos\frac{\varphi}{4} + \sin\frac{\varphi}{4}\right)^{1/n}} \quad (2)$$

where r and φ are the polar coordinates and n and l are parameters to be fitted. φ ranges from 0 to 2π. Shi et al. (2018a) demonstrated that these two parameters could be mathematically expressed by leaf width and length. The area of the SGE was then equal to:

$$A = \frac{1}{2}\int_0^{2\pi} r^2 d\varphi \quad (3)$$

When n is a constant for different individual leaves, the following will be true: $A \propto L^2$ (Lin et al. 2018). In other words, the ratio of leaf width to length is a constant. However, despite the fact that the leaves were from the same species, there was a certain degree of intraspecific variation in the ratio of leaf width to length (Fig. 9a). Apparently, a larger variation of the ratio of leaf width to length will result in a lower goodness of fit. Thus, Eq. (3) with a constant n can be regarded as a special case of the Montgomery model where leaf width is proportional to leaf length (namely a constant ratio of leaf width to length). The smaller n is, the smaller the estimate of the Montgomery parameter is; and vice versa. When n goes to infinity, r will be a constant (= L/2) based on Equation 2. As a result, Eq. (3) is actually the area of a circle. This means that the Montgomery parameter equals π/4. Triangular leaves could be considered to be another extreme form of leaf shape in plants. For truly triangular leaves, the Montgomery parameter would be 0.5. For *Polygonum perfoliatum* L., whose leaf shape is similar to that of an equilateral triangle (Kumar and DiTommaso 2005), our estimate of the Montgomery parameter was 0.55 (Fig. 10a). In fact, the shape of the leaves of *P. perfoliatum* is better described as hastate, which describes the shape of an arrow with a pair of outward-pointed lobes at its base. This may explain why the observed Montgomery parameter exceeds 0.5. Interestingly, the estimate of the exponent of leaf area-length allometry of this plant approaches 2 (Fig. 10b).

Leaf shape is essentially determined by genes (Sicard et al. 2014), and the leaf shape diversity of the Brassicaceae family for instance is related to regulatory evolution coupled with gene duplication and loss by modifying local growth pattern during organogenesis (Vlad et al. 2014). However, the veins also play a significant role on blade growth directions (Runions et al. 2017). A hub-and-spoke vein pattern usually leads to a circular leaf shape, e.g. the common pennywort (*Hydrocotyle vulgaris* L.), so that the distance from any point on the leaf edge to its center approaches a constant to keep a high transformation efficiency of water, inorganic salts and nutrients. Most leaf shapes, such as deltoid, lobed, ovate, obovate, palmate and truncate, are related to the dendritic vein pattern. The areas of these leaves are obviously smaller than that of an ellipse whose major axis is defined as leaf

length and minor axis is defined as leaf width. Although there are some leaves whose shapes approach an ellipse, the part at the base or at the tip is usually narrower than that at the converse position (at tip or at base), which results in an asymmetrical 'elliptical' shape. Thus, we believe that the estimates of the Montgomery parameter for different broad-leaved plants should be in the range of $(1/2, \pi/4)$.

Conclusion

We showed that the Montgomery model is well suited to calculate the area of a leaf by using its length and width. Different leaf shapes did not affect the model accuracy, which further provided important insight to uncover the secret of the leaf-area allometry. However, additional species with extreme leaf shapes should be included in future studies to test if the Montgomery model qualifies as the most robust model for all leaf shapes. Our findings also further advance our knowledge about leaf morphologies and correlation between leaf dimensions. The Montgomery model was the most parsimonious of all our models tested and thus allows for easy application for leaf area calculations. That makes the Montgomery model particularly useful for application in field studies as it provides highly accurate estimates of leaf area based on its length and width. Leaf area is one of the most important plant traits, but *in situ* measurements and measurements under remote field conditions still impose major challenges. Knowledge about robust models predicting leaf area from easily measured leaf dimensions, as width and length, could solve those problems.

Author contribution statement ML, JS, XY, PW, LZ and ZL collected the leaves and carried out the work of image processing; the manuscript were written by PS, DAR, JG and JS; PS and JS designed the experiments; PS and DAR analyzed the data. All authors read and commented on this manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Coen E, Rolland-Lagan A-G, Mathews M, Bangham JA, Prusinkiewicz P (2004) The genetics of geometry. Proc Natl Acad Sci USA 101:4728–4735. https://doi.org/10.1073/pnas.0306308101

de Swart EAM, Groenwold R, Kanne HJ, Stam P, Marcelis LFM, Voorrips RE (2004) Non-destructive estimation of leaf area for different plant ages and accessions of *Capsicum annuum* L. J Hortic Sci Biotech 79:764−770. https://doi.org/10.1080/14620316.2004.11511840

Dornbusch T, Watt J, Baccar R, Fournier C, Andrieu B (2011) A comparative analysis of leaf shape of wheat, barley and maize using an empirical shape model. Ann Bot 107:865−873. https://doi.org/10.1093/aob/mcq181

Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman and Hall/CRC, New York, USA

Fang YM (1994) Geographical distribution and spatial pattern of *Liriodendron chinense* (Hemsl.) Sarg. J Nanjing For Univ 18(2):13–18 **(in Chinese with English Abstract)**

Gielis J (2003) A generic geometric transformation that unifies a wide range of natural and abstract shapes. Am J Bot 90:333–338. https://doi.org/10.3732/ajb.90.3.333

Gielis J (2017) The geometrical beauty of plants. Atlantis Press, Paris, France

Griffith DM, Quigley KM, Anderson TM (2016) Leaf thickness controls variation in leaf mass per area (LMA) among grazing-adapted grasses in Serengeti. Physiol Ecol 181:1035–1040. https://doi.org/10.1007/s00442-016-3632-3

Jani TC, Misra DK (1966) Leaf area estimation by linear measurements in *Ricinus communis*. Nature 212:741–742. https://doi.org/10.1038/212741b0

Kumar V, DiTommaso A (2005) Mile-a-minute (*Polygonum perfoliatum*): an increasingly problematic invasive species. Weed Technol 19:1071−1077. https://doi.org/10.1614/WT-04-177R.1

Li G, Yang D, Sun S (2008) Allometric relationships between lamina area, lamina mass and petiole mass of 93 temperate woody species vary with leaf habit, leaf form and altitude. Funct Ecol 22:557−564. https://doi.org/10.1111/j.1365-2435.2008.01407.x

Lin S, Zhang L, Reddy GVP, Hui C, Gielis J, Ding Y, Shi P (2016) A geometrical model for testing bilateral symmetry of bamboo leaf with a simplified Gielis equation. Ecol Evol 6:6798−6806. https://doi.org/10.1002/ece 3.2407

Lin S, Shao L, Hui C, Song Y, Reddy GVP, Gielis J, Li F, Ding Y, Wei Q, Shi P (2018) Why does not the leaf weight-area allometry of bamboos follow the 3/2-power law? Front Plant Sci 9:583.

https://doi.org/10.3389/fpls.2018.00583

Milla R, Reich PB (2007) The scaling of leaf area and mass: The cost of light interception increases with leaf size. Proc R Soc B 274:2109−2114. https://doi.org/10.1098/rspb.2007.0417

Montgomery EG (1911) Correlation studies in corn. In: Annual Report no. 24. Agricultural Experimental Station, Lincoln, NB, 108–159

O'Shea B, Mordue-Luntz AJ, Fryer RJ, Pert CC, Bricknell IR (2006) Determination of the surface area of a fish. J Fish Dis 29:437−440. https://doi.org/10.1111/j.1365-2761.2006.00728.x

Palaniswamy KM, Gomez KA (1974) Length-width method for estimating leaf area of rice. Agron J 66:430–433. https://doi.org/10.2134/agronj1974.00021962006600030027x

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167−234. https://doi.org/10.1071/BT12225

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Runions A, Tsiantis M, Prusinkiewicz P (2017) A common developmental program can produce diverse leaf shapes. New Phytol 216:401−418. https://doi.org/10.1111/nph.14449

Sandhu HS, Shi PJ, Kuang XJ, Xue FS, Ge F (2011) Applications of the bootstrap to insect physiology. Fla Entomol 94:1036−1041. https://doi.org/10.1653/024.094.0442

Shi PJ, Liu MD (2018) Taylor's power law of the leaf bilateral symmetry measure of *Liriodendron* trees. J Nanjing For Univ in press **(in Chinese with English Abstract)**

Shi PJ, Huang JG, Hui C, Grissino-Mayer HD, Tardif J, Zhai LH, Wang FS, Li BL (2015a) Capturing spiral radial growth of conifers using the superellipse to model tree-ring geometric shape. Front Plant Sci 6:856. https://doi.org/10.3389/fpls.2015.00856

Shi PJ, Xu Q, Sandhu HS, Gielis J, Ding YL, Li HR, Dong XB (2015b) Comparison of dwarf bamboos (*Indocalamus sp.*) leaf parameters to determine relationship between spatial density of plants and total leaf area per plant. Ecol Evol 5:4578−4589. https://doi.org/10.1002/ece3.1728

Shi PJ, Ratkowsky DA, Wang NT, Li Y, Reddy GVP, Zhao L, Li B-L (2017) Comparison of five methods for parameter estimation under Taylor's power law. Ecol Complex 32:121−130. https://doi.org/10.1016/j.ecocom.2017.10.006

Shi PJ, Ratkowsky DA, Li Y, Zhang LF, Lin SY, Gielis J (2018a). General leaf-area geometric formula exists for plants − Evidence from the simplified Gielis equation. Forests 9:714. https://doi.org/10.3390/f9110714

335 Shi PJ, Zheng X, Ratkowsky DA, Li Y, Wang P, Cheng L (2018b) A simple method for measuring the bilateral
336 symmetry of leaves. Symmetry 10:118. https://doi.org/10.3390/sym10040118
337 Sicard A, Thamm A, Marona C, Lee YW, Wahl V, et al. (2014) Repeated evolutionary changes of leaf
338 morphology caused by mutations to a homeobox gene. Curr Biol 24:1880−1886.
339 https://doi.org/10.1016/j.cub.2014.06.061
340 Sun J, Fan R, Niklas KJ, Zhong Q, Yang F, Li M, Chen X, Sun M, Cheng D (2017) "Diminishing returns" in the
341 scaling of leaf area vs. dry mass in Wuyi Mountain bamboos, Southeast China. Am J Bot 104:993−998.
342 https://doi.org/10.3732/ajb.1700068
343 Thompson DW (1917) On growth and form. Cambridge University Press, London, UK
344 Tian F, Wang Y, Sandhu HS, Gielis J, Shi P (2018) Comparison of seed morphology of two ginkgo cultivars. J
345 For Res in press. https://doi.org/10.1007/s11676-018-0770-y
346 Verwijst T, Wen DZ (1996) Leaf allometry of *Salix viminalis* during the first growing season. Tree Physiol
347 16:655−660
348 Vlad D, Kierzkowki D, Rast MI, Vuolo F, Dello Ioio R, Galinha C, et al. (2014). Leaf shape evolution through
349 duplication, regulatory diversification, and loss of a homeobox gene. Science 343:780−783.
350 https://doi.org/10.1126/science.1248384
351 Wang P, Ratkowsky DA, Xiao X, Yu XJ, Su JL, Zhang LF, Shi PJ (2018) Taylor's power law for leaf bilateral
352 symmetry. Forests 9:500. https://doi.org/10.3390/f9080500
353 Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227.
354 https://doi.org/10.1023/a:1004327224729
355 Witkowski ETF, Lamont BB (1991) Leaf specific mass confounds leaf density and thickness. Oecologia 88:86–
356 493. https://doi.org/10.1007/BF00317710
357 Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, et al. (2004) The worldwide leaf economics
358 spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403
359 Yano S, Terashima I (2004) Developmental process of sun and shade leaves in *Chenopodium album* L. Plant Cell
360 Environ 27:781–793. https://doi.org/10.1111/j.1365-3040.2004.01182.x
361

Figure legends

Fig. 1 Comparison of the leaf-area observed and predicted values of the 10 geographical populations of *P. subaequalis*. *A* represents leaf area; *L* represents leaf length; *W* represents leaf width; RMSE represents the root-mean-square error; *r* represents the correlation coefficient of the observed and predicted values of leaf area; *n* represents the sample size of leaves; $\exp(\hat{a}_1)$ represents the estimate of the Montgomery parameter; 95% CI represents the 95% confidence interval of the Montgomery parameter. Population 'XX' represents the population code (see Table S1 in Electronic Supplementary Material for details).

Fig. 2 Comparison of the leaf-area observed and predicted values of the 5 species of Lauraceae. *A* represents leaf area; *L* represents leaf length; *W* represents leaf width; RMSE represents the root-mean-square error; *r* represents the correlation coefficient of the observed and predicted values of leaf area; *n* represents the sample size of leaves; $\exp(\hat{a}_1)$ represents the estimate of the Montgomery parameter; 95% CI represents the 95% confidence interval of the Montgomery parameter (see Table S2 in Electronic Supplementary Material for details).

Fig. 3 Comparison of the leaf-area observed and predicted values of American and Chinese tulip trees and their hybrid. *A* represents leaf area; *L* represents leaf length; *W* represents leaf width; RMSE represents the root-mean-square error; *r* represents the correlation coefficient of the observed and predicted values of leaf area; *n* represents the sample size of leaves; $\exp(\hat{a}_1)$ represents the estimate of the Montgomery parameter; 95% CI represents the 95% confidence interval of the Montgomery parameter (see Table S3 in Electronic Supplementary Material for details).

Fig. 4 Comparison of the leaf-area observed and predicted values of the 5 species of Oleaceae. *A* represents leaf area; *L* represents leaf length; *W* represents leaf width; RMSE represents the root-mean-square error; *r* represents the correlation coefficient of the observed and predicted values of leaf area; *n* represents the sample size of leaves; $\exp(\hat{a}_1)$ represents the estimate of the Montgomery parameter; 95% CI represents the 95% confidence interval of the Montgomery parameter (see Table S4 in Electronic Supplementary Material for details).

Fig. 5 Comparison of the leaf-area observed and predicted values of the 12 bamboo species. *A* represents leaf area; *L* represents leaf length; *W* represents leaf width; RMSE represents the root-mean-square error; *r* represents the correlation coefficient of the observed and predicted values of leaf area; *n* represents the sample size of leaves; $\exp(\hat{a}_1)$ represents the estimate of the Montgomery parameter; 95% CI represents the 95% confidence interval of the Montgomery parameter (see Table S5 in Electronic Supplementary Material for details).

Fig. 6 Comparison of the leaf-area observed and predicted values of the 12 species of Rosaceae. *A* represents leaf area; *L* represents leaf length; *W* represents leaf width; RMSE represents the root-mean-square error; *r*

392 represents the correlation coefficient of the observed and predicted values of leaf area; *n* represents the sample size
393 of leaves; $\exp(\hat{a}_1)$ represents the estimate of the Montgomery parameter; 95% CI represents the 95% confidence
394 interval of the Montgomery parameter (see Table S6 in Electronic Supplementary Material for details).
395 **Fig. 7** Comparison of the leaf-area observed and predicted values of the six classes of plants. The open circles
396 in every panel represent the pooled data of each class of plants; different colors represent different species (or
397 different geographical populations of the same species for the first panel) in every panel.
398 **Fig. 8** Comparison of the estimates of the Montgomery parameter among the six classes of plants. The letters A,
399 B, C, D, E and F on the top of each box exhibit the significance of difference. A > B > C > D > E > F.
400 **Fig. 9** Boxplot of the ratios of leaf width to length among 47 data sets from six classes of plants and the
401 relationship between the coefficient of variation in the *W/L* ratios and root-mean-square error. The numbers on or
402 below the boxplot in panel **a** represent the coefficients of variation in the ratio of leaf width to length; the numbers
403 around the regression straight line in panel **b** represent RMSE values corresponding to different CV values for 47
404 data sets.
405 **Fig. 10** Comparison of the predicted results using the actual leaf data of *P. perfoliatum* and simulated leaf data.
406 Panel **a** exhibits the 95% confidence interval (CI) of the estimate of the Montgomery parameter (namely the
407 intercept), and panel **b** exhibits the 95% confidence interval (CI) of the estimate of the slope.
408

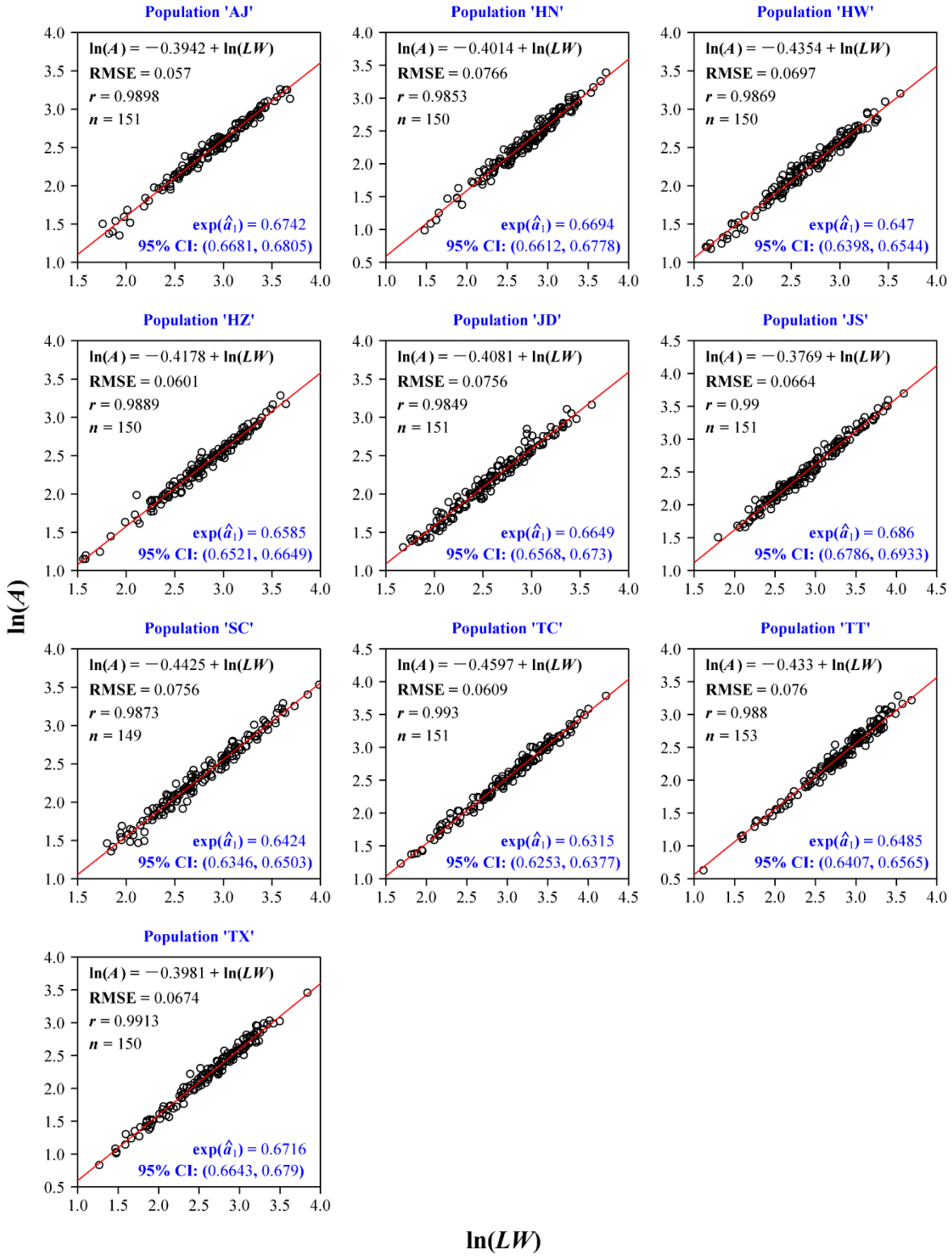
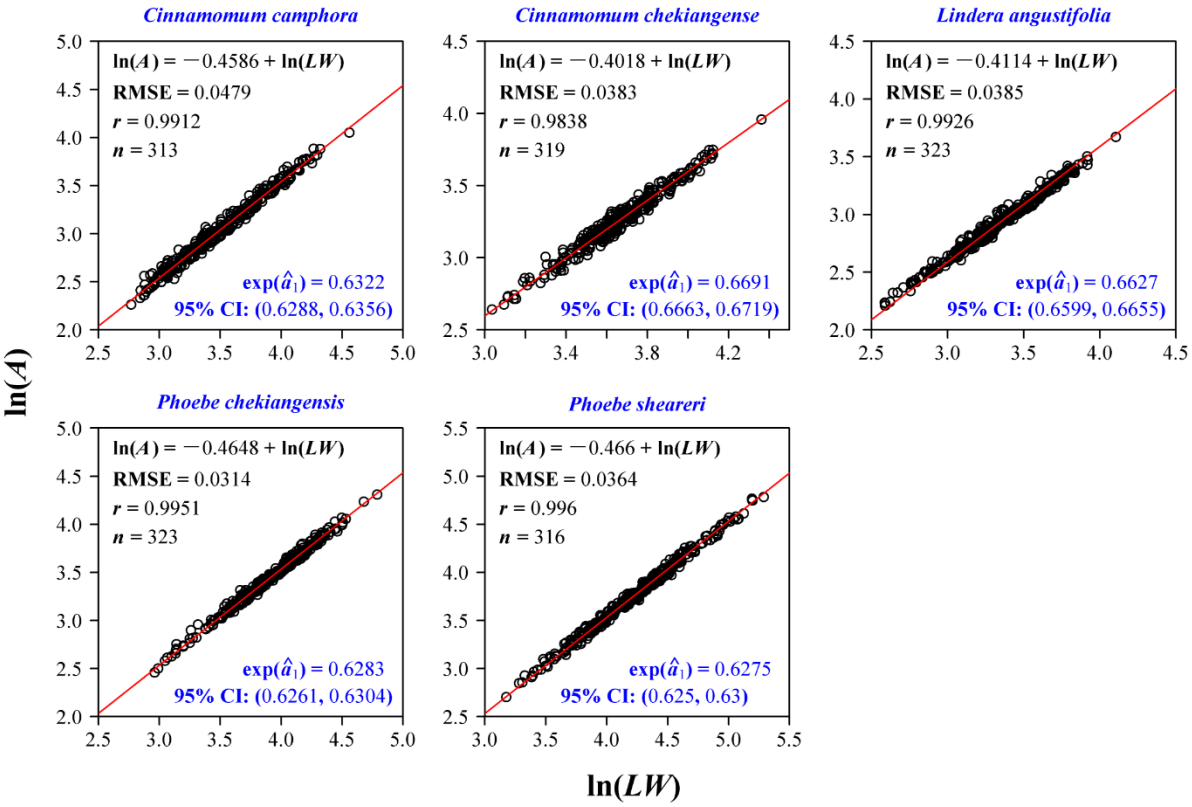

Population 'AJ'
ln(A) = −0.3942 + ln(LW)
RMSE = 0.057
r = 0.9898
n = 151
exp(â1) = 0.6742
95% CI: (0.6681, 0.6805)
Population 'HN'
ln(A) = −0.4014 + ln(LW)
RMSE = 0.0766
r = 0.9853
n = 150
exp(â1) = 0.6694
95% CI: (0.6612, 0.6778)
Population 'HW'
ln(A) = −0.4354 + ln(LW)
RMSE = 0.0697
r = 0.9869
n = 150
exp(â1) = 0.647
95% CI: (0.6398, 0.6544)
Population 'HZ'
ln(A) = −0.4178 + ln(LW)
RMSE = 0.0601
r = 0.9889
n = 150
exp(â1) = 0.6585
95% CI: (0.6521, 0.6649)
Population 'JD'
ln(A) = −0.4081 + ln(LW)
RMSE = 0.0756
r = 0.9849
n = 151
exp(â1) = 0.6649
95% CI: (0.6568, 0.673)
Population 'JS'
ln(A) = −0.3769 + ln(LW)
RMSE = 0.0664
r = 0.99
n = 151
exp(â1) = 0.686
95% CI: (0.6786, 0.6933)
Population 'SC'
ln(A) = −0.4425 + ln(LW)
RMSE = 0.0756
r = 0.9873
n = 149
exp(â1) = 0.6424
95% CI: (0.6346, 0.6503)
Population 'TC'
ln(A) = −0.4597 + ln(LW)
RMSE = 0.0609
r = 0.993
n = 151
exp(â1) = 0.6315
95% CI: (0.6253, 0.6377)
Population 'TT'
ln(A) = −0.433 + ln(LW)
RMSE = 0.076
r = 0.988
n = 153
exp(â1) = 0.6485
95% CI: (0.6407, 0.6565)
Population 'TX'
ln(A) = −0.3981 + ln(LW)
RMSE = 0.0674
r = 0.9913
n = 150
exp(â1) = 0.6716
95% CI: (0.6643, 0.679)
ln(A)
ln(LW)

Fig. 1



412

413 **Fig. 2**

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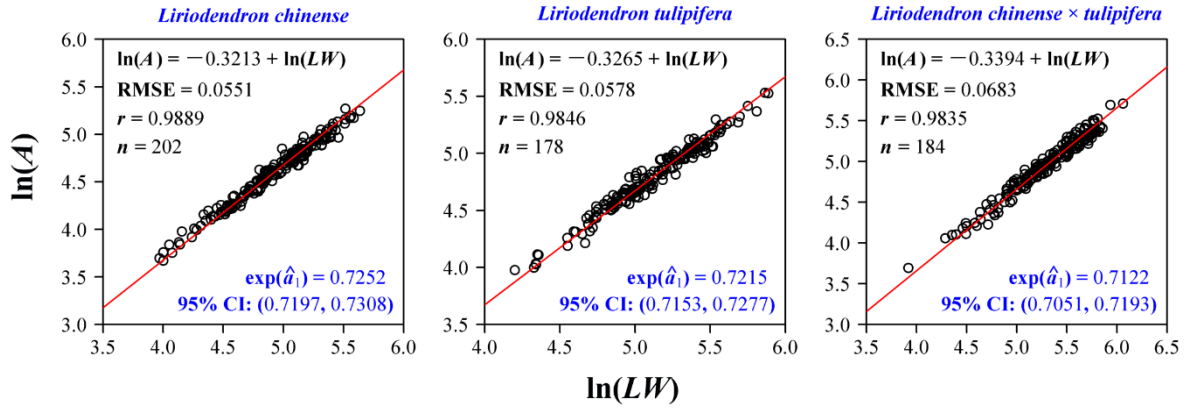

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416 **Fig. 3**

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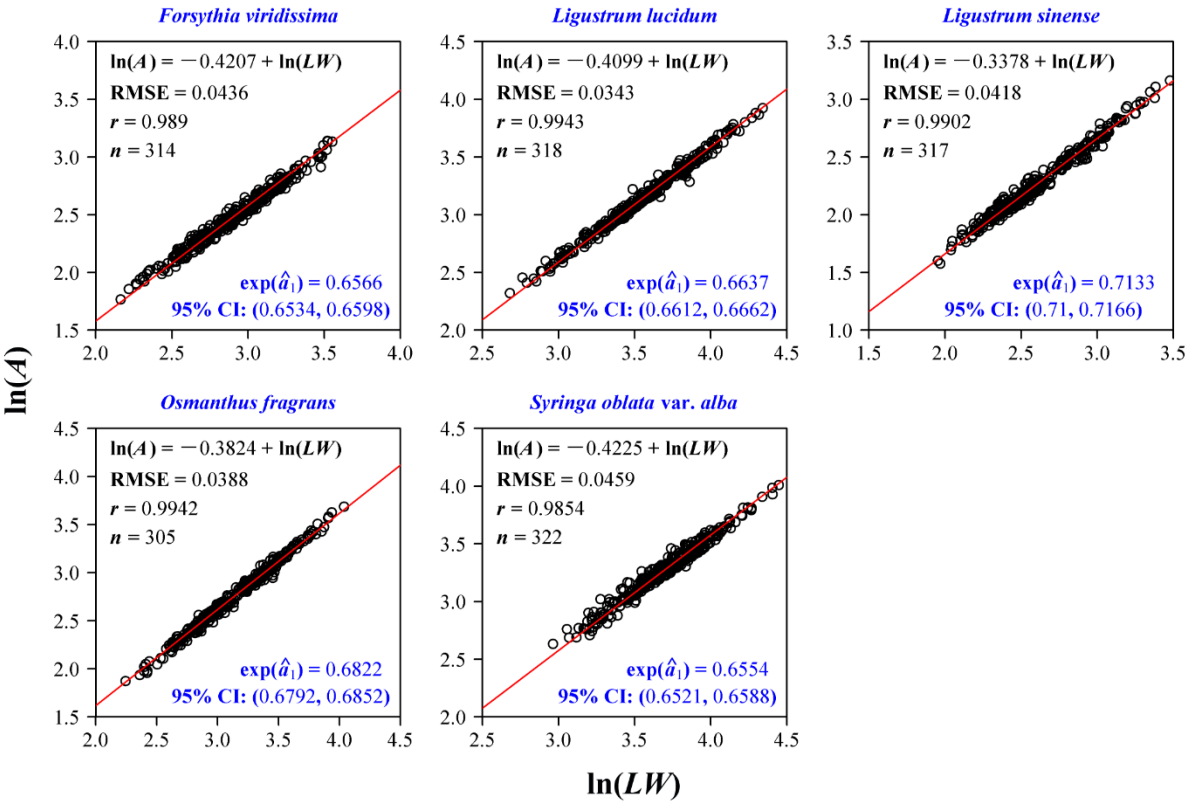

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419 **Fig. 4**

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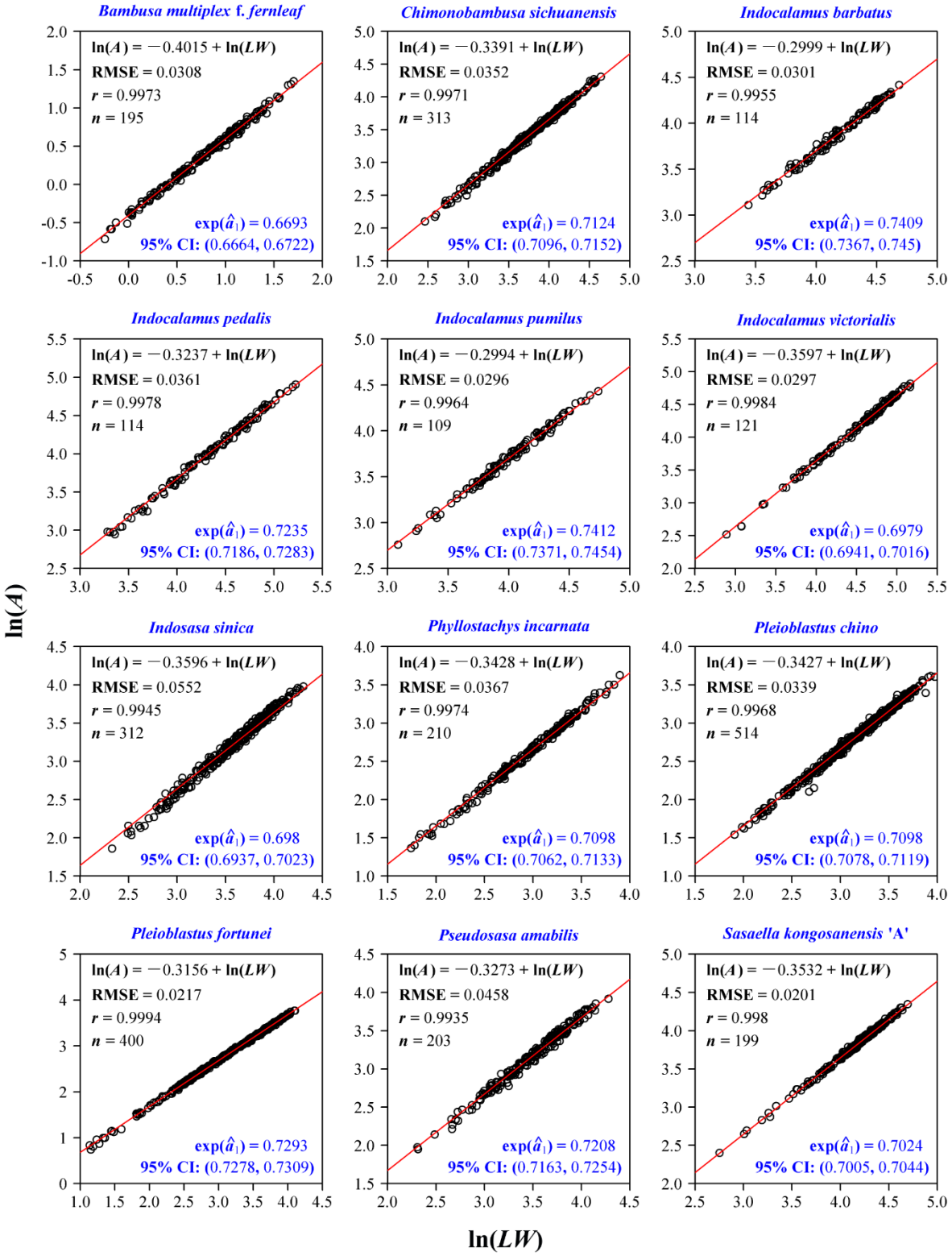

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422 **Fig. 5**

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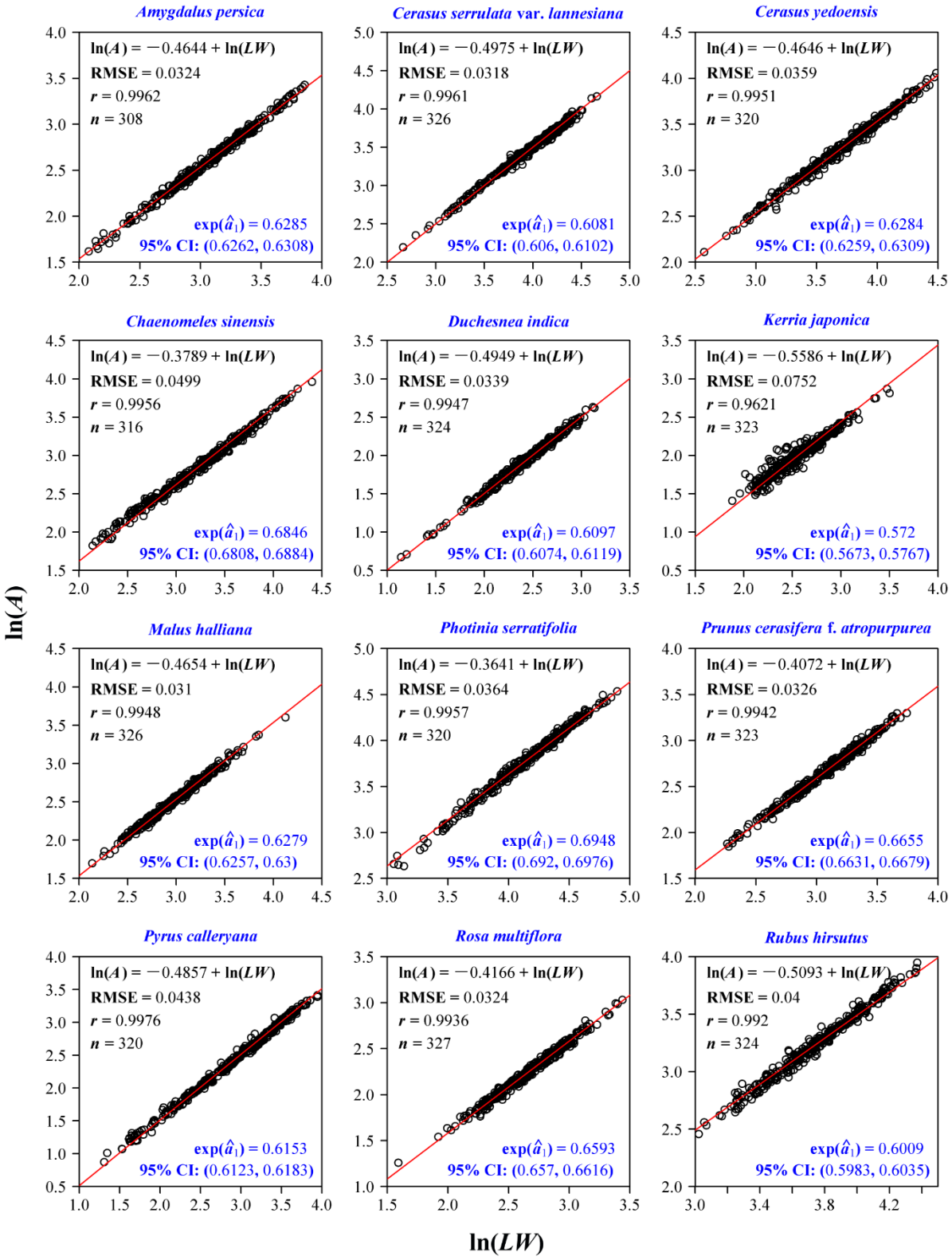
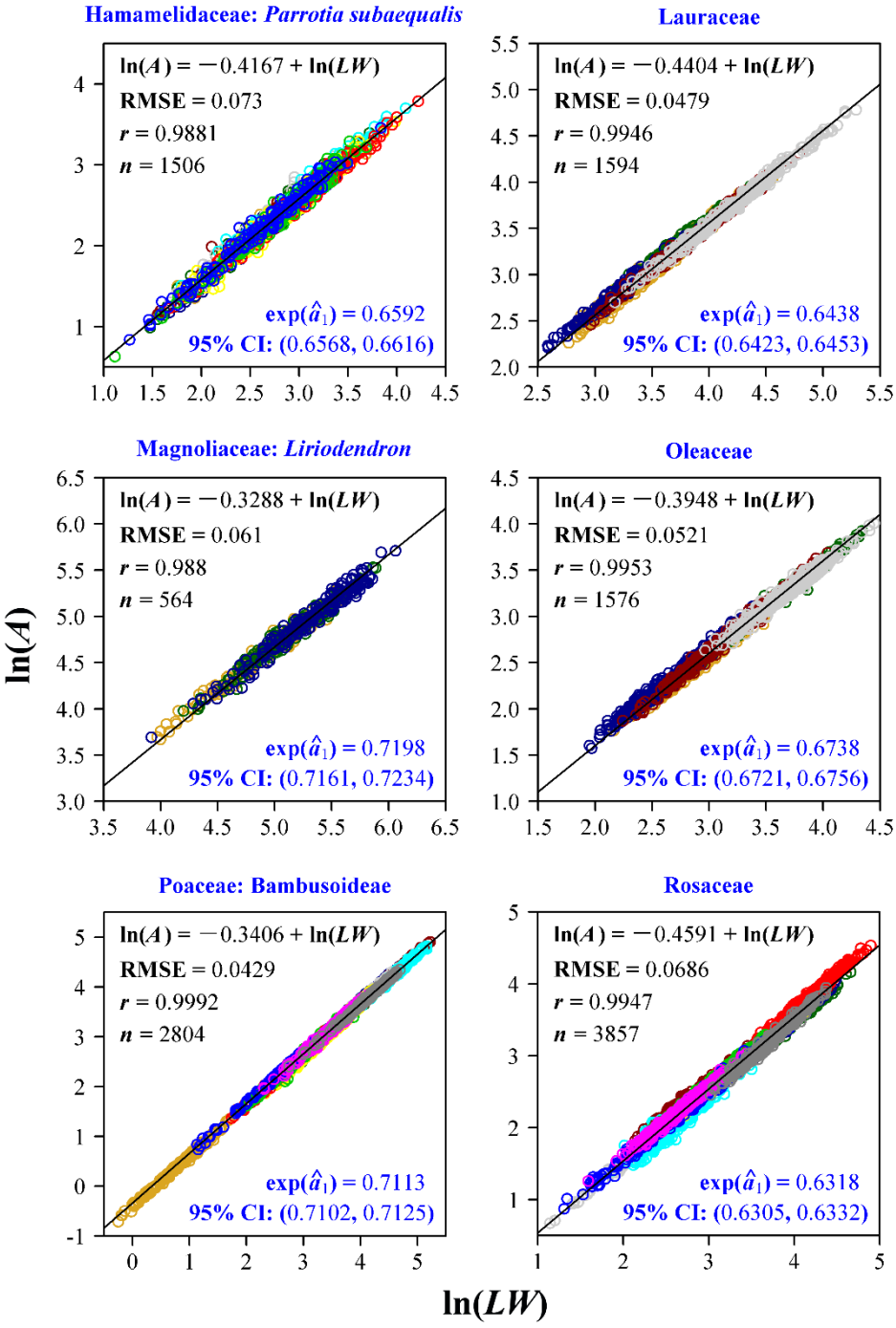

Amygdalus persica
ln(A) = −0.4644 + ln(LW)
RMSE = 0.0324
r = 0.9962
n = 308
exp(â1) = 0.6285
95% CI: (0.6262, 0.6308)
Cerasus serrulata var. lannesiana
ln(A) = −0.4975 + ln(LW)
RMSE = 0.0318
r = 0.9961
n = 326
exp(â1) = 0.6081
95% CI: (0.606, 0.6102)
Cerasus yedoensis
ln(A) = −0.4646 + ln(LW)
RMSE = 0.0359
r = 0.9951
n = 320
exp(â1) = 0.6284
95% CI: (0.6259, 0.6309)
Chaenomeles sinensis
ln(A) = −0.3789 + ln(LW)
RMSE = 0.0499
r = 0.9956
n = 316
exp(â1) = 0.6846
95% CI: (0.6808, 0.6884)
Duchesnea indica
ln(A) = −0.4949 + ln(LW)
RMSE = 0.0339
r = 0.9947
n = 324
exp(â1) = 0.6097
95% CI: (0.6074, 0.6119)
Kerria japonica
ln(A) = −0.5586 + ln(LW)
RMSE = 0.0752
r = 0.9621
n = 323
exp(â1) = 0.572
95% CI: (0.5673, 0.5767)
Malus halliana
ln(A) = −0.4654 + ln(LW)
RMSE = 0.031
r = 0.9948
n = 326
exp(â1) = 0.6279
95% CI: (0.6257, 0.63)
Photinia serratifolia
ln(A) = −0.3641 + ln(LW)
RMSE = 0.0364
r = 0.9957
n = 320
exp(â1) = 0.6948
95% CI: (0.692, 0.6976)
Prunus cerasifera f. atropurpurea
ln(A) = −0.4072 + ln(LW)
RMSE = 0.0326
r = 0.9942
n = 323
exp(â1) = 0.6655
95% CI: (0.6631, 0.6679)
Pyrus calleryana
ln(A) = −0.4857 + ln(LW)
RMSE = 0.0438
r = 0.9976
n = 320
exp(â1) = 0.6153
95% CI: (0.6123, 0.6183)
Rosa multiflora
ln(A) = −0.4166 + ln(LW)
RMSE = 0.0324
r = 0.9936
n = 327
exp(â1) = 0.6593
95% CI: (0.657, 0.6616)
Rubus hirsutus
ln(A) = −0.5093 + ln(LW)
RMSE = 0.04
r = 0.992
n = 324
exp(â1) = 0.6009
95% CI: (0.5983, 0.6035)
ln(A)
ln(LW)

Fig. 6



427

428 **Fig. 7**

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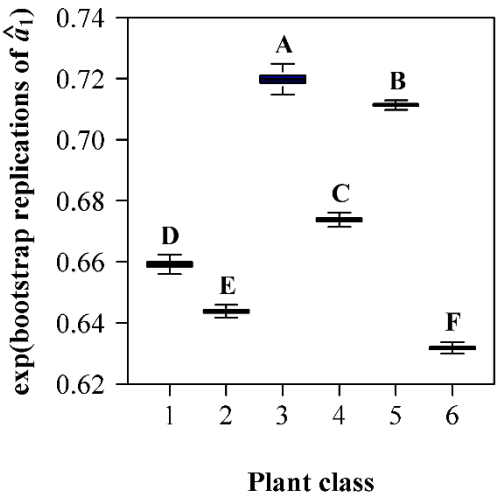

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431 **Fig. 8**

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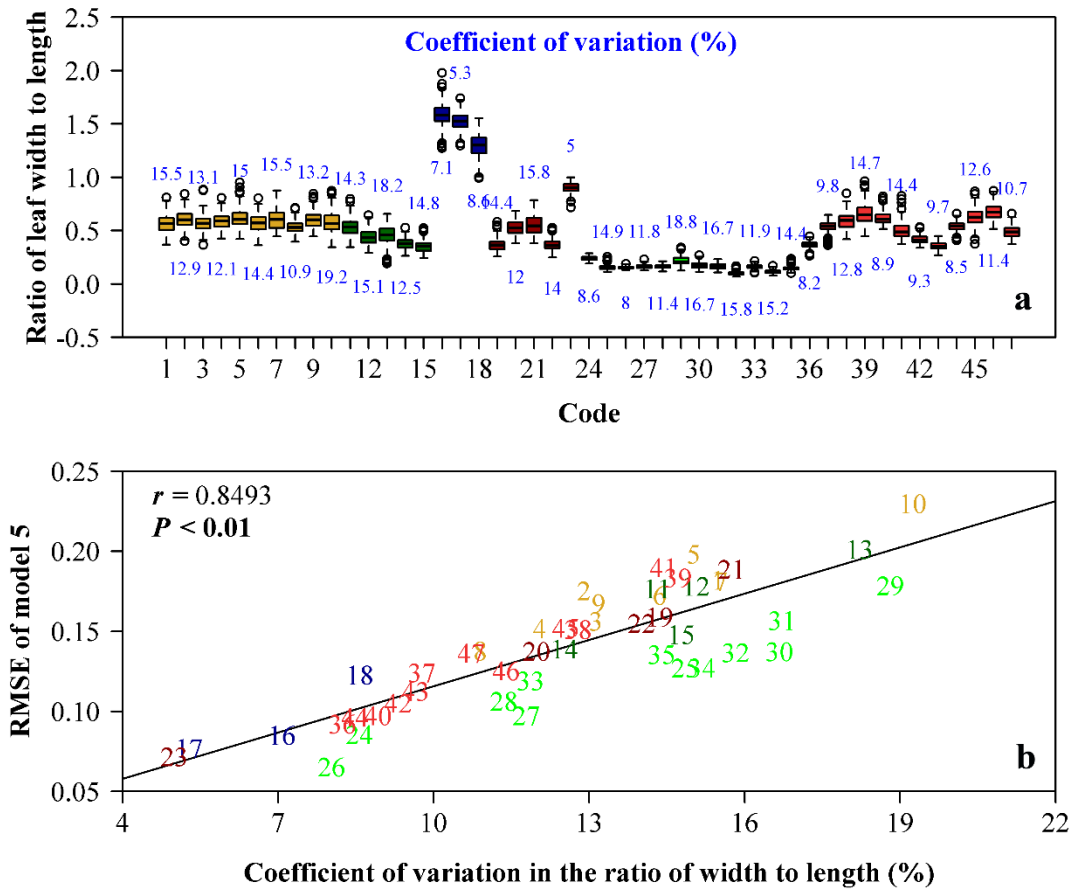

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434 **Fig. 9**

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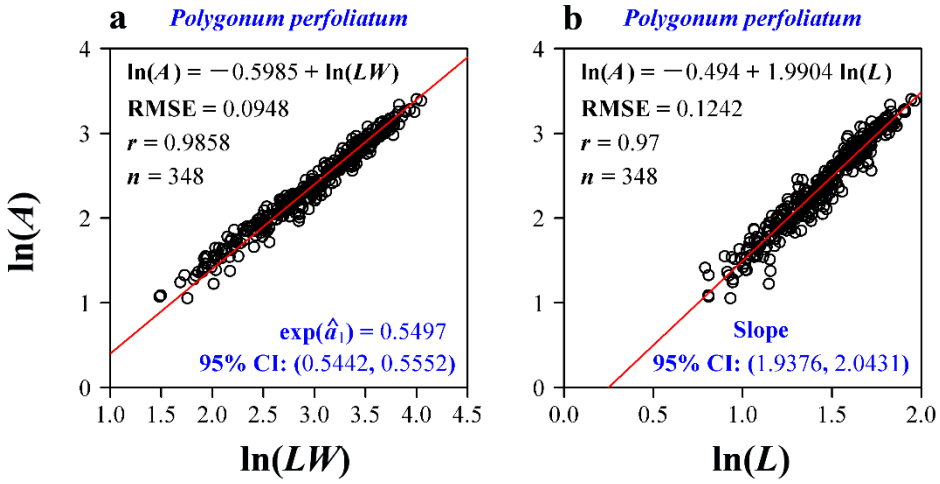

436

437 **Fig. 10**

438

439 **Table(s)**

440 **Table 1** Six leaf-area allometric models used in this study.

Model no.	Model	Log-transformed model
Model 1	$A = c_1(LW)$	$\ln(A) = a_1 + \ln(LW)$
Model 2	$A = c_2(LW)^{b_2}$	$\ln(A) = a_2 + b_2 \ln(LW)$
Model 3	$A = c_3\ L^{b_3}$	$\ln(A) = a_3 + b_3 \ln(L)$
Model 4	$A = c_4\ W^{b_4}$	$\ln(A) = a_4 + b_4 \ln(W)$
Model 5	$A = c_5\ L^2$	$\ln(A) = a_5 + 2\ln(L)$
Model 6	$A = c_6\ W^2$	$\ln(A) = a_6 + 2\ln(W)$

441 Here, for the first model, $c_1 = \exp(a_1)$, and there are the similar relationships between the pre-exponential
442 constants and the intercepts for the other models. *A* represents leaf area; *L* represents leaf length; *W* represents leaf
443 width; the other letters represents constants to be fitted.

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Electronic Supplementary Material

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