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Original Research Article

Lamina shape does not correlate with lamina surface area: An analysis based on the simplified Gielis equation

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ABSTRACT

The simplified Gielis equation (SGE) can approximately describe the leaf shapes of many different broad-leaved plant species by replacing two parameters of the SGE with leaf width and leaf length with a floating ratio (c -value) to adjust for leaf length. In this study, we tested the validity of the SGE in predicting leaf area using 20 bamboo species, 12 species of Rosaceae, 5 species of Lauraceae, and 5 species of Oleaceae. We find that c -values in leaf length for 20 bamboo species are all smaller than zero, whereas, for most tree species, c -values are larger than zero. Using c -values, there was a strong correlation (>0.99 for most of the species investigated) between actual and predicted leaf area. Also, using the SGE to fit the leaf profile data, the predicted leaf width approaches its actual value, whereas the predicted length is larger than or smaller than its actual value (for bamboo species and most tree species, respectively). Although c -values ranged from -15% to zero for bamboo species and from zero to 17% for tree species, the mean percent error in leaf area for most species did not exceed 5% . These findings indicate that leaves exhibit more variation in length than in width, i.e., leaf area is fairly conservative despite considerable variation in leaf shape. Given that the SGE adequately describes the areas of leaves with complex forms (e.g., several species of Rosaceae), our data indicate that the SGE is a useful tool for describing leaf morphometrics and may open a door for the study of leaf shape evolution.

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1. Introduction

The land plants first appeared in the mid-Palaeozoic about 470 million years ago (Kenrick and Crane, 1997; Brown and Lemmon, 2011; Harholt et al., 2016; Niklas, 2016), with large multivascularized leaves (“megaphylls”) making their first appearance about 430 million years ago (Kenrick and Crane, 1997; Tomescu, 2009; Becker et al., 2012; Harrison and Morris, 2018). Despite their considerable diversity across extant tracheophyte lineages, species within the same taxon typically have the same or very similar leaf shape. For example, the leaves of bamboo species are morphologically very similar, with

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differences in shape mainly reflected in the quotient of leaf width to length (Lin et al., 2016, 2018; Shi et al., 2019a, 2019b). In contrast, leaf shape can differ, sometimes significantly within the same taxon (and even on the same plant) and cannot be distinguished simply by the quotient of leaf width to length, e.g. species of Rosaceae (Shi et al., 2019a; Yu et al., 2019). The extent to which leaf shape varies, both within and across higher taxa is important because it can affect photosynthesis, transpiration, and other important functional traits (Calvin and Benson, 1948; Gates, 1965; Crosbie et al., 2008; Wright et al., 2017). For example, photosynthetic potentials are closely associated with leaf (lamina) surface area, which is reported to scale as the 2/3 to 1/1 power of leaf dry mass (Milla and Reich, 2007; Niklas et al., 2007; Huang et al., 2019). Likewise, plant metabolic rates are reported to scale to leaf mass as a power less than one (Makarieva et al., 2004; Shi et al., 2014). Thus, leaf area is an important proxy for estimating the productivity of plant communities (Garkoti, 2008), analyzing interspecific plant competition (Givnish, 1987), and evaluating plant adaptation to environmental changes (Greenwood, 1992; Jacobs, 1999; Hovenden and Vander Schoor, 2006; Díaz et al., 2016).

Clearly, an accurate and efficient method to quantify the relationship between leaf area and shape is required. Although there are many methods for measuring leaf area, the traditional method is to scan leaves using some automatic software. Although this method is highly accurate, it is time-consuming and sometimes prone to result in irreversible damage of specimens. In addition, it is impossible to continuously observe changes in leaf area attending leaf growth and development. An alternative method for measuring leaf area directly is the application of software installed in smartphones (e.g., Schrader et al., 2017), which can obtain accurate measurements of leaf area when the requirements of operation are met, such as the separation of target leaves from other leaves and the necessity to set strict contrasts between leaf and background color. In addition, this method more or less requires flat leaf surfaces. A third approach to calculate leaf area is based on other leaf morphological measures, especially leaf length and width. Many investigators have attempted to find a mathematical relationship between leaf area and either or both of these parameters, particularly for vegetables (Robbins and Pharr, 1987; Guo and Sun, 2001; Salerno et al., 2005), crops (Dornbusch et al., 2011), and fruits (Mendoza-de Gyves et al., 2007; Beslic et al., 2010; Roupheal et al., 2010; Sala et al., 2015). Shi et al. (2019a, 2019b) used 12000 leaves from 41 species to demonstrate that there is a proportional relationship between leaf area and the product of leaf length and width both at the individual species level and at the family level (i.e., the pooled data). For each data set, leaf surface area can be expressed as a proportionality of the rectangle encompassing leaf length and width (Shi et al., 2019a, 2019b). Shi et al. (2018) further demonstrated that the simplified Gielis equation (SGE) (Shi et al., 2015; Lin et al., 2016) can describe the leaf margins of 5 tree species and 48 bamboo species and that the two parameters of the SGE can be expressed as leaf length and width. However, the actual leaf length is prone to deviate from the predicted value using the SGE. After adding an adjusted coefficient of leaf length, Shi et al. (2018) found that the predicted leaf area approximates the actual leaf area quite well, i.e., the measurement error did not exceed 6% of the actual leaf area. The results of these studies to describe leaf shape indicate that leaf length is more variable than leaf width both within and across the species. However, whether this phenomenon extends to other or all species remains problematic because the sample size for tree species was insufficient (Shi et al., 2018).

Here, we examined 22 tree species within three families as well as 20 bamboo species (with ca. 300 leaves per species) to determine whether the SGE is proficient at estimating leaf area and whether leaf width is more conservative than leaf length. In addition, we used a more accurate measure for leaf width relative to the method used by Shi et al. (2018).

2. Materials and methods

2.1. Leaf collection and measurement

Leaves from 42 species in four families (i.e., 20 species of Bambusoideae (Poaceae), 5 species of Lauraceae, 5 species of Oleaceae, and 12 species of Rosaceae) were collected on the Nanjing Forestry University campus (32°04'34.53"N, 118°48'42.06"E) from May to September in 2018 (see Table S1–S4 in the online supplementary material 1 for detailed collection date, scientific name and sample size for each species). Figs. 1–3 provide examples of the leaves used in this study. The university campus was used as a single collection site to reduce the influence of spatial heterogeneity and climate, which can significantly affect leaf size and shape as well as other functional traits (Pickett and Cadenasso, 1995; Peppe et al., 2011; Yin et al., 2015; Wright et al., 2017).

Fresh leaves were picked from healthy plants and subsequently wrapped in wet paper placed within plastic self-sealing bags (280 mm × 200 mm). Petioles were removed, and the remaining laminae were measured using an Aficio scanner (MP 7502; Ricoh, Tokyo, Japan) to scan each leaf into a bitmap image at 400 dpi resolution (Fig. 4a). Photoshop CS6 was then used to outline the lamina margin and to fill it with white (Fig. 4b). The Matlab procedure developed by Shi et al. (2018) was then used to extract the planar coordinates of the leaf margin (Fig. 4c), and a revised R script based on the earlier version proposed by Shi et al. (2018) was used to measure leaf area, length, and width. The revised R script defined leaf width as W_2 , where W_2 represents the maximum vertical distance between two points on the leaf margin perpendicular to the straight line through leaf base and apex (Fig. 5). The distance from the leaf base to apex was defined as leaf length. This script is provided online (see the supplementary material 2).

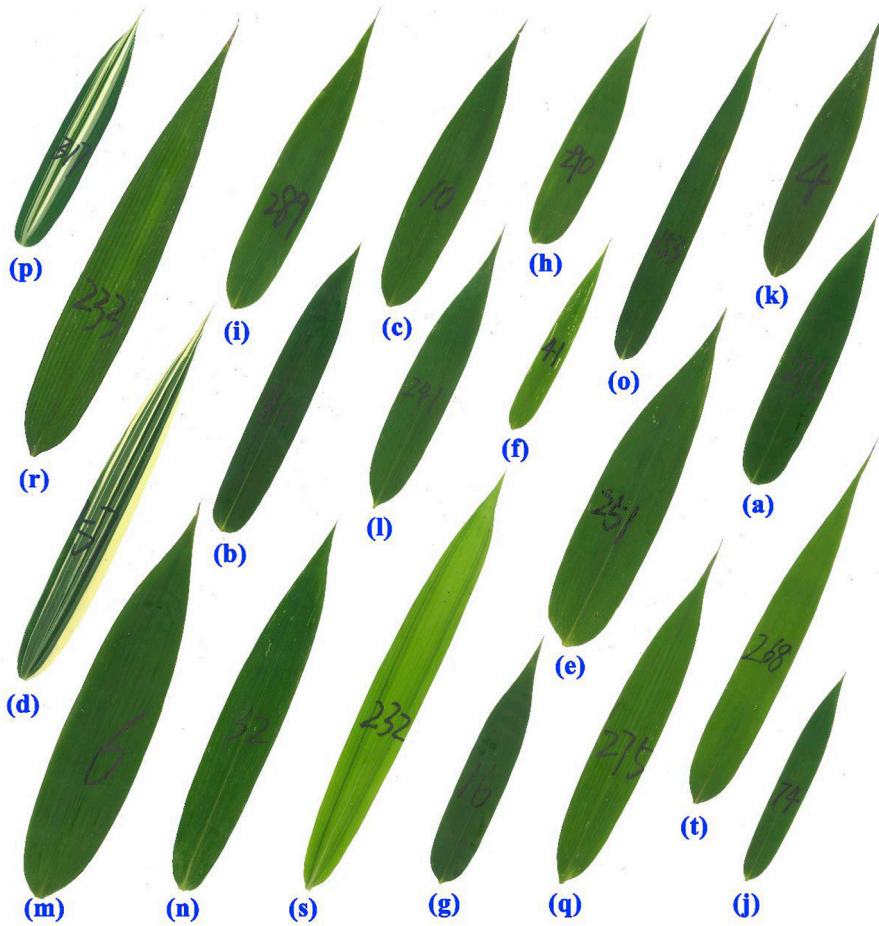


Fig. 1. Examples of leaves from 20 species of Bambusoideae (Poaceae): (a) *Bambusa emeiensis* 'Viridiflavus' Hsuen et T.P. Yi, (b) *Bambusa multiplex* (Loureiro) Raeuschel ex Schultes & J. H. Schultes in Roemer & Schultes, (c) *Chimonobambusa sichuanensis* (T. P. Yi) T. H. Wen, (d) *Hibanobambus tranquillans* f. *shiroshima*, (e) *Indosasa sinica* C. D. Chu & C. S. Chao, (f) *Oligostachyum sulcatum* Z. P. Wang et G. H. Ye, (g) *Phyllostachys aureosulcata* f. *spectabilis* C. D. Chu et C. S. Cha, (h) *Phyllostachys bambusoides* f. *castillonis* (Mitford) Muroi, (i) *Phyllostachys bambusoides* f. *lacrimadeae* Keng f. et Wen, (j) *Phyllostachys bissetii* McClure, (k) *Phyllostachys iridescens* C. Y. Yao et S. Y. Chen, (l) *Phyllostachys propinqua* McClure, (m) *Phyllostachys vivax* f. *aureocaulis* N. X. Ma, (n) *Pleioblastus argenteostriatus* (Regel) Nakai, (o) *Pleioblastus chino* (Franchet et Savatier) Makino, (p) *Pleioblastus fortune* (Van Houtte) Nakai, (q) *Pleioblastus maculatus* (McClure) C. D. Chu & C. S. Chao, (r) *Pleioblastus* sp., (s) *Pleioblastus viridistriatus* Makino, and (t) *Pseudosasa amabilis* var. *convexa* Z. P. Wang & G. H. Ye.

2.2. The simplified gielis equation (SGE) with a floating ratio of leaf length

Shi et al. (2015) proposed a simplified version of the Gielis equation (Gielis, 2003, 2017) to describe the leaf profile of bamboo:

$$\rho = \frac{l}{(\cos \frac{\varphi}{4} + \sin \frac{\varphi}{4})^{1/n}} \quad (1)$$

where ρ represents a polar radius at polar angle φ (ranging from 0 to 2π), and l and n are parameters to be fitted. Leaf length (L) and width (W) were expressed as follows (Shi et al., 2018):

$$L = (1 + 2^{-0.5/n})l \quad (2)$$

$$W = 2 \sin \varphi_w \frac{L}{(1 + 2^{-0.5/n})(\cos \frac{\varphi_w}{4} + \sin \frac{\varphi_w}{4})^{1/n}} \quad (3)$$

where φ_w represents the angle associated with leaf width in the first quadrat, and parameter n is expressed as a function of φ_w (see Shi et al., [2018] for details), i.e.,

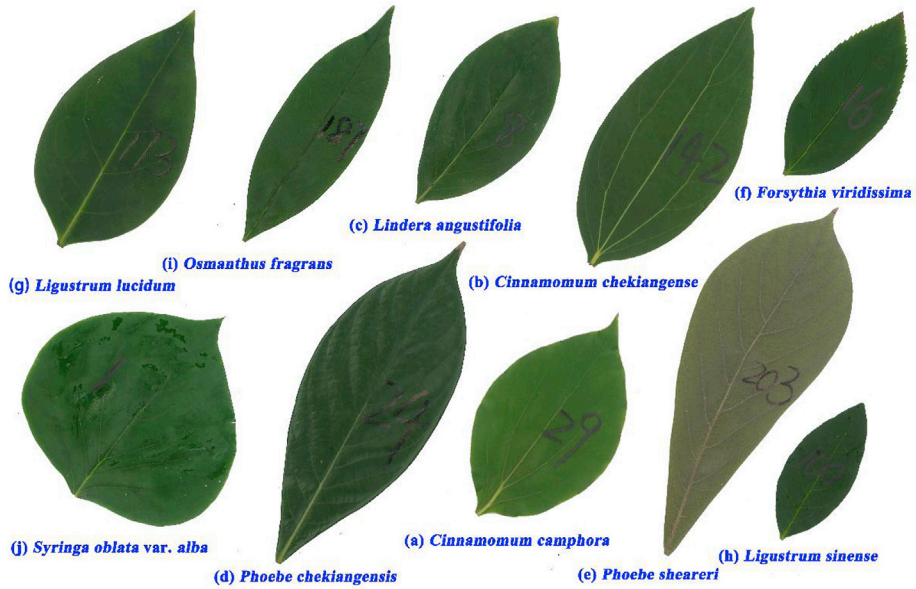


Fig. 2. Examples of leaves from 10 species of families Lauraceae (panels a–e) and Oleaceae (panels f–j) (a) *Cinnamomum camphora* (L.): J. Presl., (b) *Cinnamomum chekiangense* Nakai, (c) *Lindera angustifolia* Cheng, (d) *Phoebe chekiangensis* C. B. Shang, (e) *Phoebe sheareri* (Hemsl.) Gamble, (f) *Forsythia viridissima* Lindl., (g) *Ligustrum lucidum* Ait., (h) *Ligustrum sinense* Lour, (i) *Osmanthus fragrans* (Thunb.) Lour, and (j) *Syringa oblata* Lindl. var. *alba* Rehder.

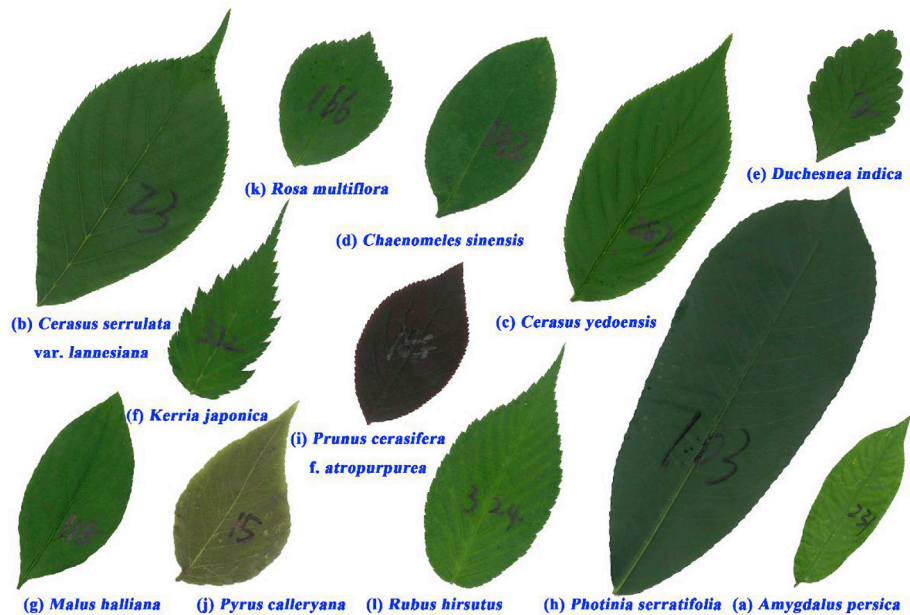


Fig. 3. Examples of leaves from 12 species of Rosaceae: (a) *Amygdalus persica* L., (b) *Cerasus serrulata* (Lindl.) G. Don ex London var. *lannesiana* (Carr.) Makino, (c) *Cerasus yedoensis* (Matsum.) Yu et Li, (d) *Chaenomeles sinensis* (Thouin) Koehne, (e) *Duchesnea indica* (Andr.) Focke (f) *Kerria japonica* (L.), DC., (g) *Malus halliana* Koehne, (h) *Photinia serratifolia* (Desf.) Kalkman, (i) *Prunus cerasifera* Ehrh. f. *atropurpurea* (Jacq.) Rehd., (j) *Pyrus calleryana*, (k) *Rosa multiflora* Thunb., and (l) *Rubus hirsutus* Thunb.

$$n = \frac{\tan\phi_w}{4} \frac{\cos\frac{\phi_w}{4} - \sin\frac{\phi_w}{4}}{\cos\frac{\phi_w}{4} + \sin\frac{\phi_w}{4}} \quad (4)$$

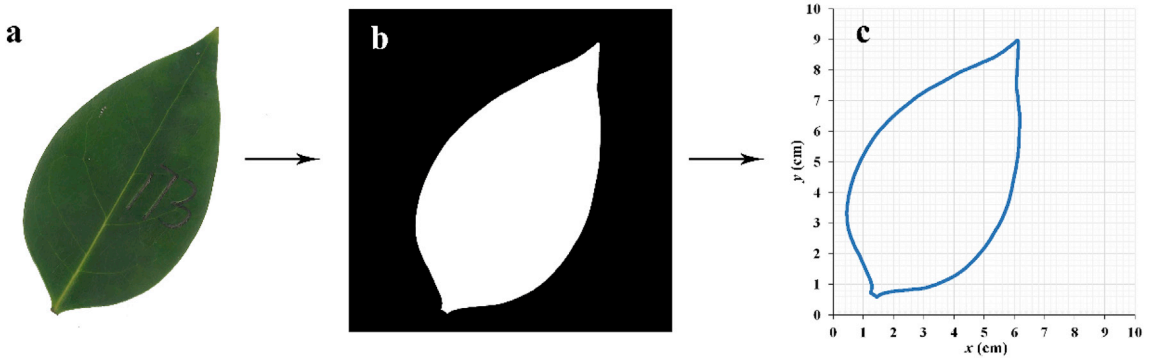


Fig. 4. Illustration of the process for extracting the planar coordinates of leaf margin.

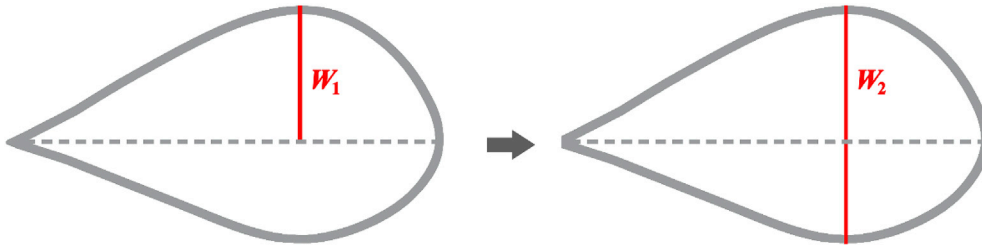


Fig. 5. Comparison of two approaches for calculating lamina length. W_1 is the length of the vertical red segment in the left panel, and W_2 is the length of the vertical red segment in the right panel. In the previous study (Shi et al., 2018) leaf width was defined as $2W_1$ regardless of whether a leaf is perfectly bilateral, whereas in the present study it was defined as W_2 . (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

When L and W are known, the numerical solution of φ_w is obtained by minimizing the absolute differences between the observed and predicted values of L and W from a group of candidate φ_w ranging from 0 to $\pi/2$ in small increments such as 10^{-6} using Eq. (2–4). The parameters n and l are determined empirically; for a polar coordinate equation, leaf area (A) is calculated using the formula

$$A = \frac{1}{2} \int_0^{2\pi} \rho^2 d\varphi = \frac{1}{2} \int_0^{2\pi} l^2 \left(\cos \frac{\varphi}{4} + \sin \frac{\varphi}{4} \right)^{-2/n} d\varphi = f(l, n) = g(L, W) \tag{5}$$

Here, f is a function of l and n , and g is a function of L and W .

Although the SGE can describe the leaf shapes of many species, there is usually an error between the actual and predicted L values (Shi et al., 2018). To cope with this limitation, a floating ratio (c) was introduced into the SGE:

$$A = g[(1 - c)L, W] \tag{6}$$

To obtain an estimate of c for each data set, we minimized the residual sum of squares (RSS) between the actual and predicted leaf areas using Eq. (6) with a group of candidates of c ranging between -20% and 20% in 0.01% increments. To compare the model's validity in calculating A among the different data sets, the mean percent error (MPE) was used:

$$\text{MPE} = \frac{\sum_{i=1}^N |(A_i - \hat{A}_i) / A_i|}{N} \times 100\% \tag{7}$$

where A_i represents the actual (scanned) leaf area of the i -th leaf, \hat{A}_i is the predicted leaf area, and N is the sample size of a data set.

2.3. Influence of the measurement error of leaf length on that of leaf area

To check the effect of the mean percent error of leaf length (MPEL) on the mean percent error of leaf area (MPEA), we set a group of the mean percent errors of leaf length ranging from 1% to 80% in 1% increments of actual leaf length. We then

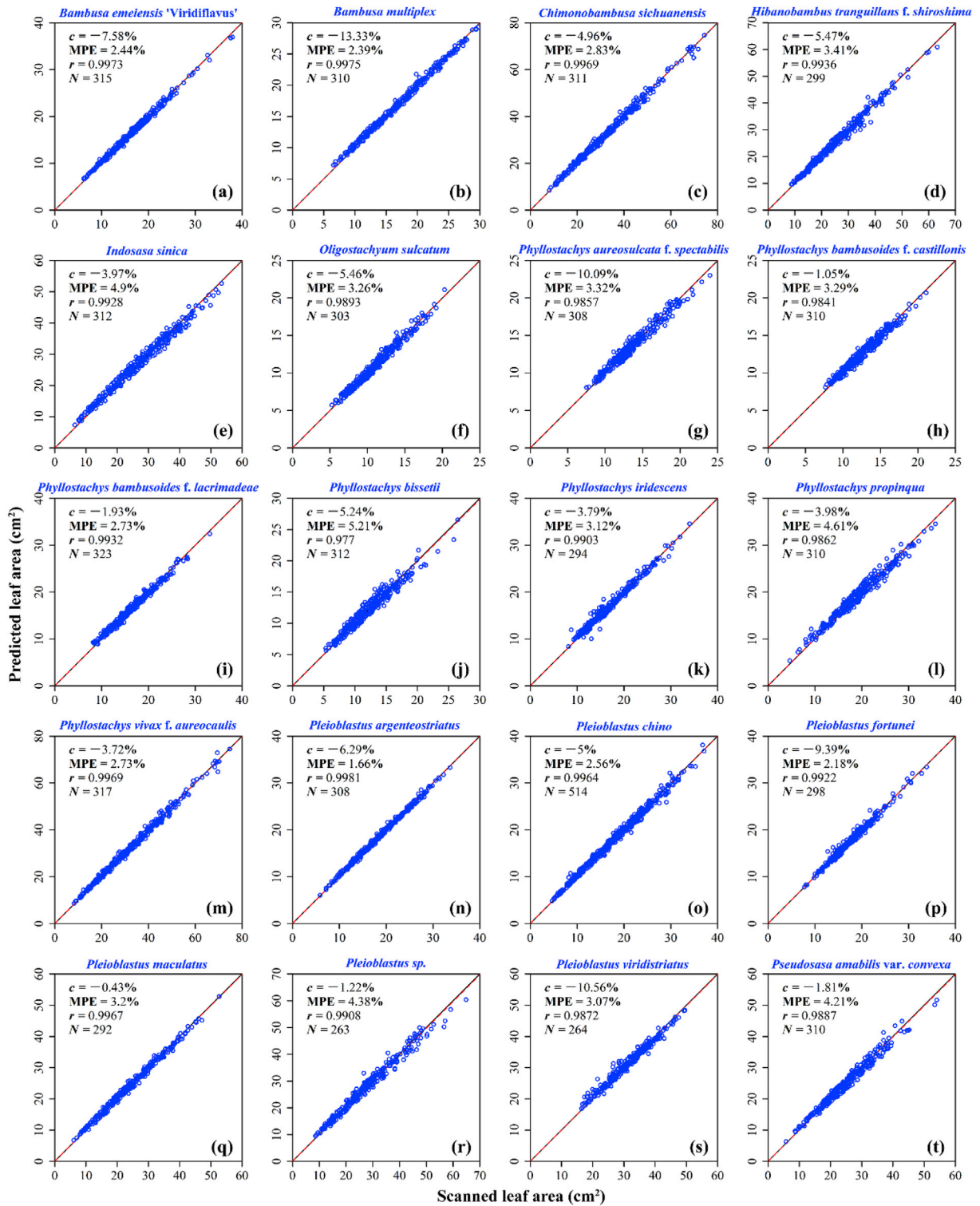


Fig. 6. Comparison between the scanned leaf area and the predicted leaf area based on the SGE for 20 species of Bambusoideae (Poaceae). The input variables used by the SGE include: (i) leaf width, (ii) leaf length and (iii) the floating ratio (c) of leaf length. The small blue open circles represent the planar coordinates consisting of the scanned leaf area (as the x-coordinate) and predicted leaf area (as the y-coordinate). The black solid line represents $y = x$, and the red dashed line represents the regression line between the scanned and the predicted leaf areas. In each panel, c represents the floating ratio of leaf length; MPE presents the mean percent error of leaf area; r represents the correlation coefficient between the scanned leaf area and predicted leaf area; and N represents the sample size (namely the number of sampled leaves). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

calculated leaf area based on the actual leaf width and an adjusted leaf length that was randomly generated from the interval $[L \times (1 - \text{MPEL}), L \times (1 + \text{MPEL})]$. The mean percent error of leaf area was then calculated based on the scanned and predicted leaf areas.

All analyses were performed using R software (R Core Team, 2015).

3. Results

The data demonstrate that the SGE is robust in describing leaf shapes across 42 plant species (Table S5 in the online supplementary material 1; Figs. S1–S3 in the online supplementary material 3). Most root-mean-square root (RMSE) values of the SGE fit were less than 0.5, with the exception of the bamboo *Pleioblastus viridistriatus* Makino.

Among the 20 bamboo species, the floating ratios fell within the range of -15% to 0 , and among them, the ratios of 11 species were greater than -5% (Fig. 6), i.e., the predicted leaf length using the SGE was slightly larger than the actual (scanned) leaf length for the bamboo species investigated. Only one species (*Phyllostachys bissetii* McClure) had a mean percent error of leaf area (MPEA) greater than 5% (Fig. 6j), and 19 species with MPEA values smaller than 5% . For the 10 Lauraceae and Oleaceae species, except for *Ligustrum sinense* Lour, the floating ratios were within the range of 0 – 15% , with 9 species whose MPEA values were smaller than 5% (Fig. 7). One species, *Syringa oblata* Lindl. var. *alba* Rehder, had a MPEA of 6.01% (Fig. 7j). Thus, except for *L. sinense*, the predicted leaf length using the SGE was smaller than the actual leaf length for each of the remaining 9 species. Across the 12 Rosaceae species, most floating ratios were within the range of 0 – 20% (Fig. 8). One exception was *Kerria japonica* (L.) DC., which had a floating ratio larger than 20% (Fig. 8f); another exception was *Photinia*

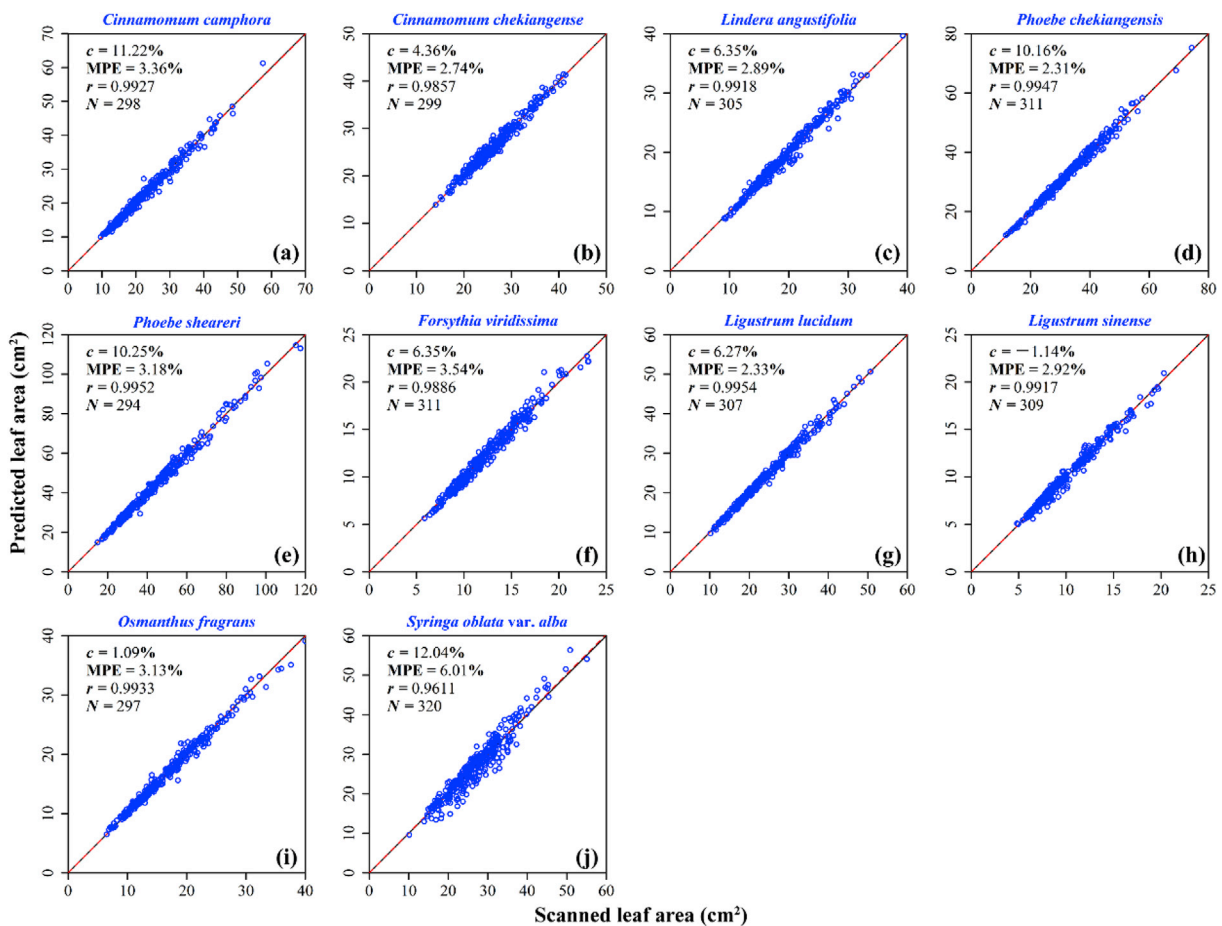


Fig. 7. Comparison between the scanned leaf area and the predicted leaf area based on the SGE for 10 species of families Lauraceae (panels a–e) and Oleaceae (panels f–j). The input variables used by the SGE include: (i) leaf width, (ii) leaf length and (iii) the floating ratio (c) of leaf length. The small blue open circles represent the planar coordinates consisting of the scanned leaf area (as the x -coordinate) and predicted leaf area (as the y -coordinate). The black solid line represents $y = x$, and the red dashed line represents the regression line between the scanned and the predicted leaf areas. In each panel, c represents the floating ratio of leaf length; MPE presents the mean percent error of leaf area; r represents the correlation coefficient between the scanned leaf area and predicted leaf area; and N represents the sample size (namely the number of sampled leaves). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

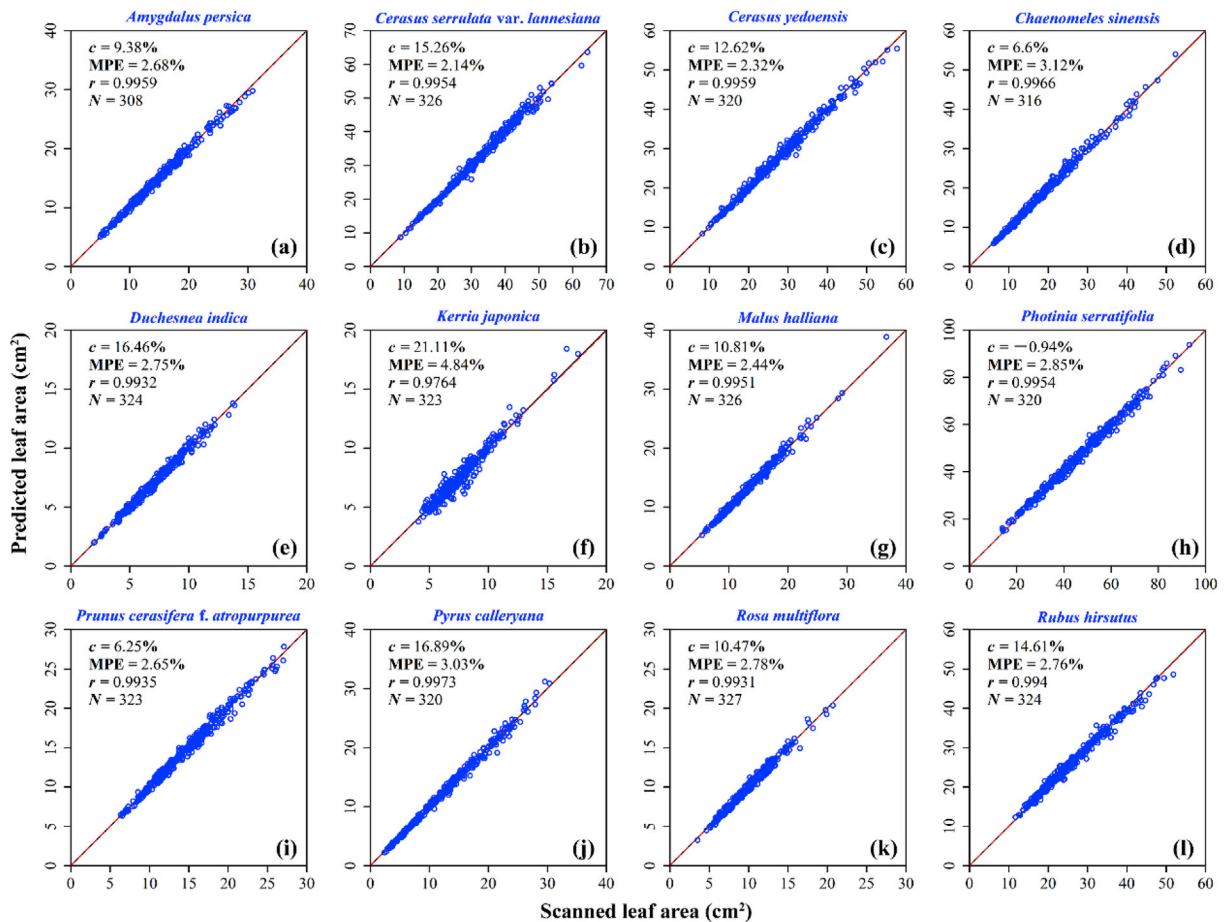


Fig. 8. Comparison between the scanned leaf area and the predicted leaf area based on the SGE for 12 species of Rosaceae. The input variables used by the SGE include: (i) leaf width, (ii) leaf length and (iii) the floating ratio (c) of leaf length. The small blue open circles represent the planar coordinates consisting of the scanned leaf area (as the x -coordinate) and predicted leaf area (as the y -coordinate). The black solid line represents $y = x$, and the red dashed line represents the regression line between the scanned and the predicted leaf areas. In each panel, c represents the floating ratio of leaf length; MPE is the mean percent error of leaf area; r is the correlation coefficient for the regression curve for the scanned versus predicted leaf area; N is the sample size (i.e., the number of sampled leaves). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

serratifolia (Desf.) Kalkman, which had a floating ratio smaller than zero (Fig. 8h). Thus, once again, except for *P. serratifolia*, the predicted leaf length using the SGE was smaller than the actual leaf length for each species among the remaining 11 Rosaceae species. The measurement errors of leaf area for the 12 species investigated were all less than 5%, although most floating ratios (8/12) exceeded 10%. Further, after introducing floating ratios, the correlation coefficients between the actual and the predicted area based on Eq. (6) were all numerically large. There were 31 species whose correlation coefficients exceeded 0.99.

MPEA was approximately equal to MPEL/2 for most bamboo species when $MPEL \geq 20\%$ (Fig. 9), i.e., the measurement error of leaf area was only half the measurement error of leaf length. When $MPEL < 20\%$, MPEA increased slowly with increasing MPEL, and the maximum of MPEA was smaller than 15%. Similar results were found for most Lauraceae and Oleaceae species (Fig. 10). However, for *S. oblata* var. *alba*, the data points deviated significantly from the $y = 1/2 x$ regression line (Fig. 10j). Also, there were three species whose MPEA vs. MPEL data points were slightly higher than the straight line (Fig. 10a,d,e). The leaf shapes of these four species especially *S. oblata* var. *alba* deviated from a standard shape predicted by the SGE (see panels a, d, e and j in Fig. S2). For the 4 Rosaceae species, leaf shape fit the SGE well, and the data points of MPEA vs. MPEL (when $MPEL \geq 20\%$) deviated little from the $y = 1/2 x$ straight line (Fig. 11d,h,i,k). However, the data points of the remaining 8 species especially *K. japonica* (Fig. 11f) did not conform well to the $y = 1/2 x$ straight line expectation.

4. Discussion

Shi et al. (2018) reported that 6 among 7 data sets for bamboo generated positive values for the floating ratio of leaf length. These results differ from those reported here, wherein negative values were observed. This discrepancy may reflect the fact

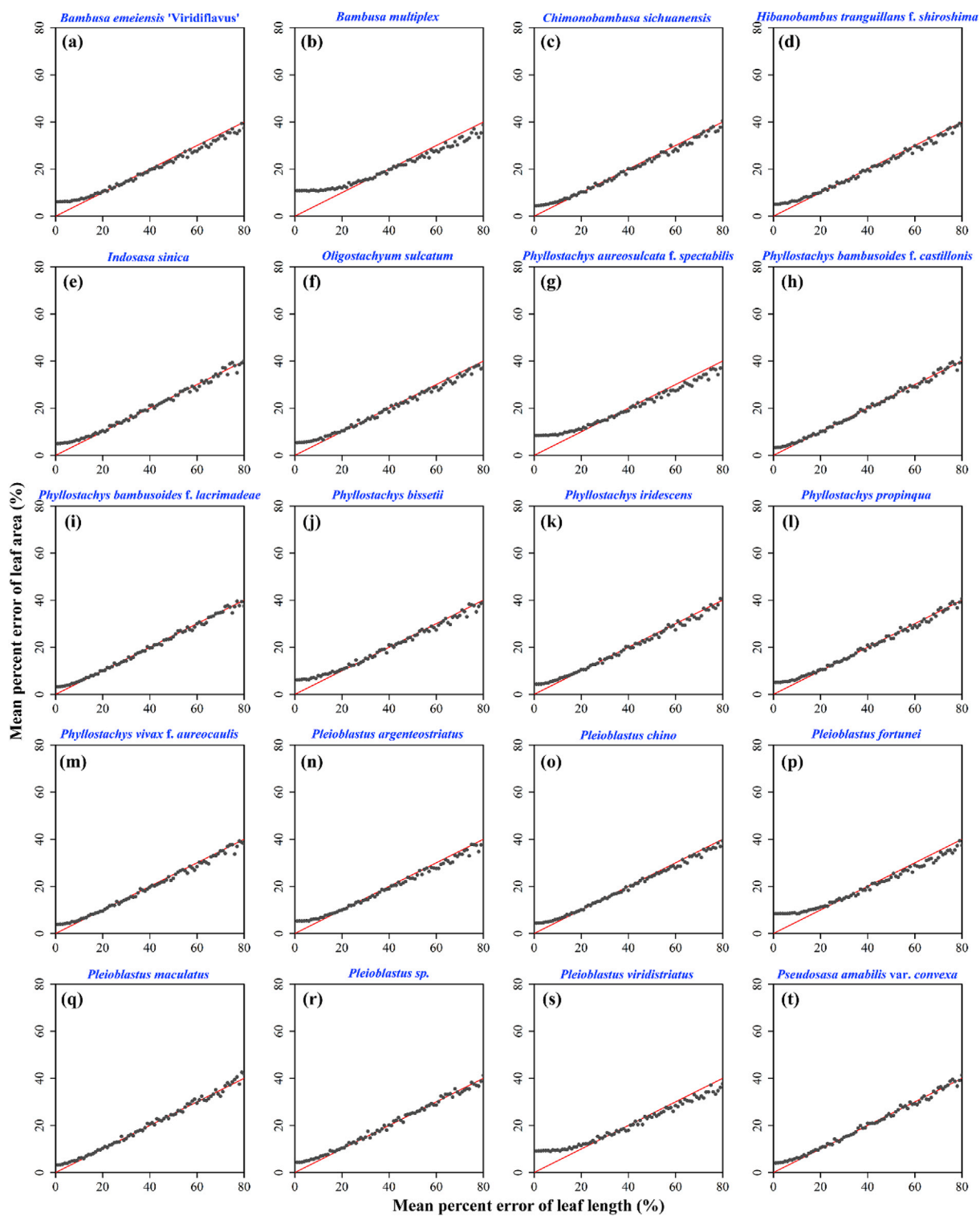


Fig. 9. Effect of the mean percent error of leaf length (MPEL) on the mean percent error of leaf area (MPEA) based on the data of 20 species of Bamboos (Poaceae). The gray points represent the data of MPEA vs. MPEL; and the red straight line represents the equation $y = 1/2 x$. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

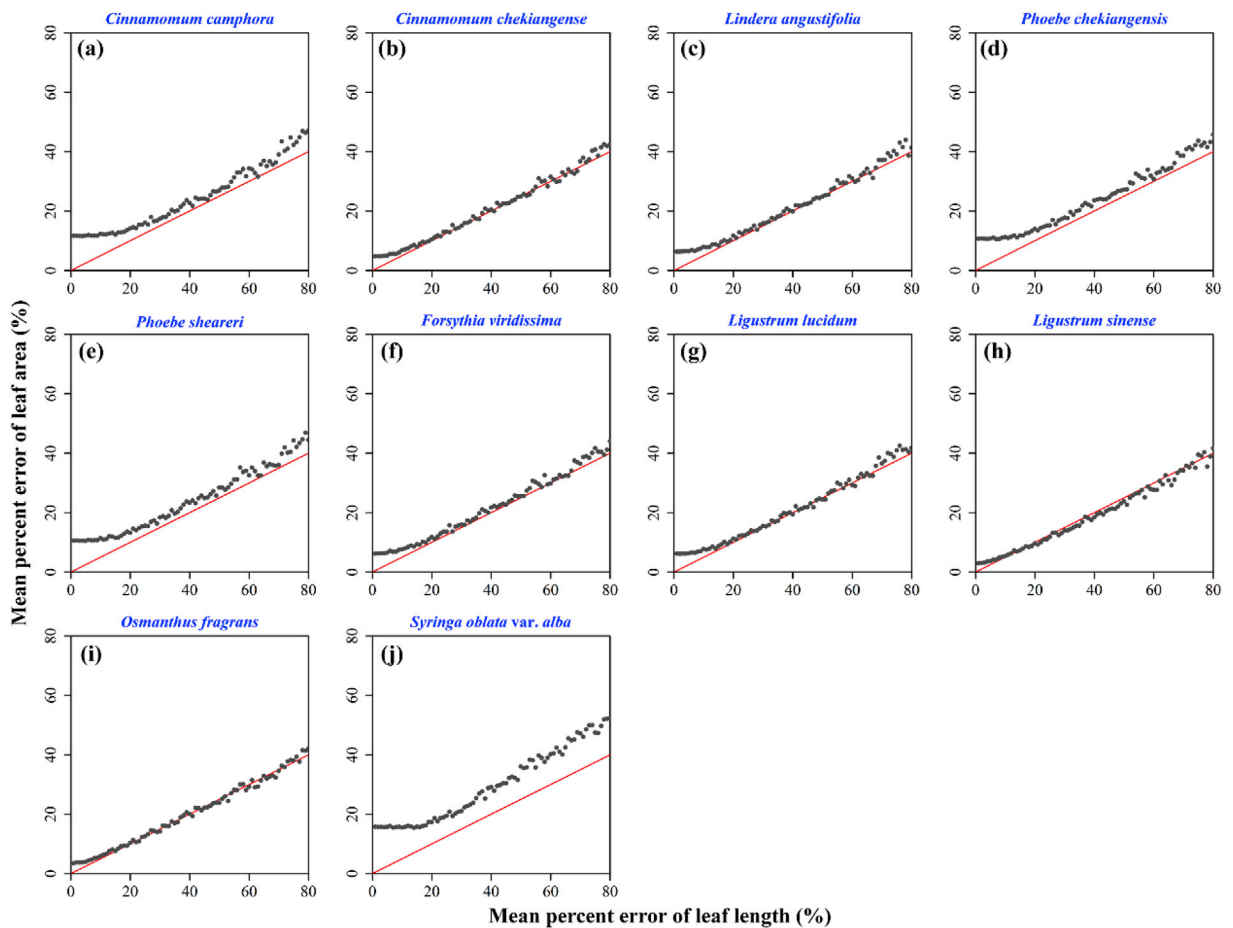


Fig. 10. Effect of the mean percent error of leaf length (MPEL) on the mean percent error of leaf area (MPEA) based on the data of 10 species of families Lauraceae (panels a–e) and Oleaceae (panels f–j). The gray points represent the data of MPEA vs. MPEL; the red straight line denotes the equation $y = 1/2 x$. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that Shi et al. (2018) defined leaf width as 2 times W_1 (see Fig. 5), whereas leaf width was defined here as W_2 . Leaf area has been demonstrated to be proportional to the product of leaf length and width, which was referred to as the Montgomery equation (Jain and Misra, 1966; Shi et al., 2019a, 2019b). If leaf width is overestimated, leaf length might be underestimated, which could result in positive values of floating leaf length ratios. The SGE actually limits the proportionality coefficient in the Montgomery equation. According to Shi et al. (2019b), the proportionality coefficients for the pooled data of 20 bamboo species is equal to 0.714. On the condition that the proportionality coefficient is a constant, an overestimated leaf width will lead to an underestimated leaf length because the product of leaf length and width is a constant in the Montgomery equation. Thus, there is reason to believe that the predicted leaf lengths of bamboo plants using the SGE will be slightly longer than those actually observed, which is implied by negative value of the floating ratio c (Fig. 6). However, for the leaves of the trees investigated over the course of this study, the converse was observed, i.e., predicted leaf lengths using the SGE are shorter than those actually observed, accompanied by a positive value of the floating ratio c (Figs. 7–8).

For 20 bamboo species and 9 Lauraceae and Oleaceae species, the leaf margin is entire (Figs. 1–2). In contrast, the leaves of *Forsythia viridissima* Lindl. (in the Oleaceae) and the 12 Rosaceae species have serrated leaf margins, which may enable leaves to maximize the utilization of light captured by augmenting reflection within the leaf lamina (Smith et al., 1997). The diversity of serrations and lobes clearly increases the complexity of leaf shape and may lead to deviations between predicted and observed leaf lengths using the SGE. However, our analyses show that serrations do not significantly negatively affect leaf area calculations using the SGE. Indeed, 11 of the 12 MPEA values reported for Rosaceae species are lower than 4% (Fig. 8), as is the case for *F. viridissima*. For *S. oblata* var. *alba* (in the Oleaceae), the MPEA exceeds 6%, although its leaf margin is entire. The leaf shape of this species is different from all the others, i.e., its leaf width exceeds leaf length, which may account for the relatively large prediction error using the SGE (Fig. S2j in the online supplementary material 3). For some plants whose leaf shape is approximately elliptical (e.g., *Hydrocotyle vulgaris* L.), the SGE is still valid (Shi et al., 2019b), indicating that variations in leaf margins do not substantially affect predicted leaf surface areas.

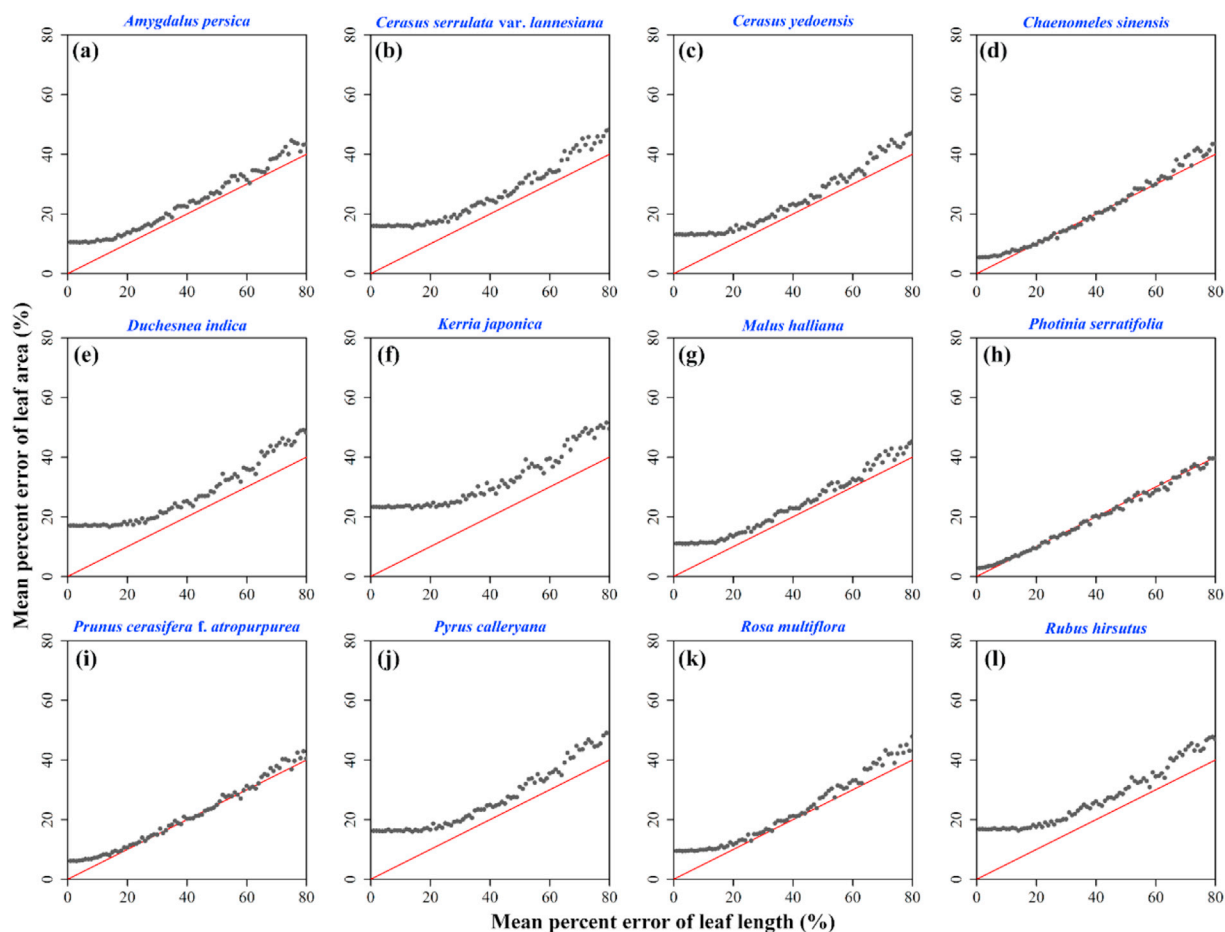


Fig. 11. Effect of the mean percent error of leaf length (MPEL) on the mean percent error of leaf area (MPEA) based on the data of 12 species of Rosaceae. The gray points represent the data of MPEA vs. MPEL; and the red straight line represents the equation $y = 1/2 x$. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

In summary, the data presented here show that the simplified Gielis equation can be used to calculate leaf area based on leaf width, length, and the floating ratio of leaf length (i.e., the adjusted coefficient of leaf length). Although the floating ratio can exceed 10% of the actual length, the measurement error of leaf area does not exceed 5% of the actual value for most of the species (40/42 > 95%) investigated in this study. When the mean percent error of leaf length (MPEL) equals or exceeds 20%, the mean percent error of leaf area (MPEA) is approximately half of the MPEL in the case of leaf shapes that are well described by the SGE. However, when the MPEL is less than 20%, the MPEA increases slowly with increasing MPEL. We conclude, therefore, that variations in leaf area are more conservative than those of leaf length, i.e., the uncertainty of 2-D measurements of leaf size is less than that of 1-D measurements of leaf size.

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Appendix A. Supplementary data

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