ELLIPTICALNESS INDEX – A SIMPLE MEASURE OF THE COMPLEXITY OF OVAL LEAF SHAPE

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Abstract

Plants have diverse leaf shapes that have evolved to adapt to the environments they have experienced over their evolutionary history. Leaf shape and leaf size can greatly influence the growth rate, competitive ability, and productivity of plants. However, researchers have long struggled to decide how to properly quantify the complexity of leaf shape. Prior studies recommended the leaf roundness index (RI = $4\pi A/P^2$) or dissection index (DI = $P/2\sqrt{\pi A}$), where P is leaf perimeter and A is leaf area. However, these two indices merely measure the extent of the deviation of leaf shape from a circle, which is usually invalid as leaves are seldom circular. In this study, we proposed a simple measure, named the ellipticalness index (EI), for quantifying the complexity of leaf shape based on the hypothesis that the shape of any oval leaf can be regarded as a variation from a standard ellipse. 2220 leaves from nine species of Magnoliaceae were sampled to check the validity of the EI. We also tested the validity of the Montgomery equation (ME), which assumes a proportional relationship between leaf area and the product of leaf length and width, because the EI actually comes from the proportionality coefficient of the ME. We also compared the ME with five other models of leaf area. The ME was found to be the best model for calculating leaf area based on consideration of the trade-off between model fit vs. complexity, which strongly supported the robustness of the EI for describing oval leaf shape. The new index can account for both leaf shape and size, and we conclude that it is a promising method for quantifying and comparing oval leaf shapes across species in future studies.

Key words: Magnoliaceae; Leaf area; Leaf length; Leaf roundness index; Leaf width.

Introduction

Leaf area is an important plant functional trait, which has attracted much attention in botany and ecology because plants can adjust the sizes of their individual leaves as an adaptation to climate change (Wright *et al.*, 2017; Baird *et al.*, 2021). Leaf shape is another important functional trait that can affect the photosynthetic efficiency of plants in the growing season and alter plant investment into structural support for different leaf areas (Royer & Wilf, 2006; Niinemets *et al.*, 2007). Although leaf shape is highly variable across different plant species, it can be represented by the ratio of leaf width (*W*) to length (*L*) for many broad-leaved plants, especially those with oval-shaped leaves (Shi *et al.*, 2021b). The leaf *W/L* ratio has been demonstrated to be associated with leaf relative water content and the scaling exponent of the leaf dry mass vs. leaf area relationship (Lin *et al.*, 2020). In addition to the aforementioned importance of the quotient of *W* and *L* in describing leaf shape, the product of *L* and *W* has been found to be proportional to leaf area (*A*) (Montgomery, 1911; Kemp, 1960; Jani & Misra, 1966; Verwijst & Wen, 1996; Shi *et al.*, 2019a, 2021a; Yu *et al.*, 2020; Schrader *et al.*, 2021). The Montgomery equation (ME) is a function that describes this proportional relationship between *A* and *LW*, and the proportionality coefficient within this function is referred to as the correction factor or the Montgomery parameter (MP). The ME has been demonstrated to apply to a large number of flat- and broad-leaved plants, regardless of the complexity of their leaf shape, and most empirical values of the MP range from 1/2 to $\pi/4$ (Shi *et al.*, 2019a; Yu *et al.*, 2020; Schrader *et al.*, 2021). The MP is thought to be closely related to leaf shape. For instance, the herb *Persicaria perfoliata* (L.) H. Gross, with triangular leaves, has an MP value of approximately 1/2 (Shi *et al.*, 2019b). However, the MP values of plants with non-standard oval leaves are usually smaller than $\pi/4$ (Shi *et al.*, 2019a).

In the investigation of leaf shape, the leaf roundness index (RI = $4\pi A/P^2$) and leaf dissection index (DI = $P/2\sqrt{\pi A}$), where *P* is the leaf perimeter, are usually proposed and used as measures of leaf shape complexity (Kincaid & Schneider, 1983; Thomas & Bazzaz, 1996; Niinemets, 1998; Santiago & Kim, 2009; Peppe *et al.*, 2011). However, the leaf RI only measures the deviation of a leaf's shape from a standard circle. If one attempts to compare leaf shapes across species that do not have approximately round leaves, the leaf RI has no meaning, aside from the possibility that the degree of roundness might influence leaf economics or physiology. In general, a reticulate leaf venation network with a star-shaped topology (e.g., the aquatic herb *Hydrocotyle vulgaris* L.) is likely to produce an approximately round leaf shape (Shi *et al.*, 2019b). However, dendritic hierarchical reticular venation patterns can generate more complex leaf shapes in which there can be large

variation in the distance of the leaf margin from the midrib along the axis from the leaf base to the apex, including the occurrence of leaf marginal teeth, serrations, dissections, and lobes (Runions *et al.*, 2017). In fact, a circle actually represents a special case of an ellipse with both foci located at the same point, and thus an index of leaf shape based on an ellipse rather than a standard circle may have broader applicability.

In the present study, we developed a simple leaf shape index for quantifying the complexity of oval leaf shape relative to a standard ellipse. In addition, we attempted to further relate this new index to the calculation of leaf size. The leaves of four *Magnolia* species and five *Michelia* species (Magnoliaceae) were used to test the validity of the newly developed leaf shape index, as well as that of related leaf area models.

Materials and Methods

Tree species and leaf collection: The leaves of nine species of Magnoliaceae with oval-shaped leaves were chosen as study materials. The trees sampled were grown in two adjacent sites in Nanjing, Jiangsu Province, China. The two sites are 3.4 km apart, and there is no strong spatial heterogeneity between them. We sampled 130 to 380 leaves from the middle canopy of 3–5 trees of each species from July to September in 2019 and 2020. Detailed leaf sampling information is listed in Table 1. As soon as leaves were collected from trees, they were wrapped in wet newspaper, enclosed in transparent self-sealing plastic bags (28 cm × 20 cm), and taken to the laboratory to be scanned. Strictly speaking, a complete tree leaf includes both the leaf petiole and lamina. However, in the present study, we did not consider the leaf petiole, and referred to the lamina as the leaf for simplicity. To clearly exhibit leaf

shape and its possible link to leaf venation network type, we chemically remove epidermal and mesophyll tissues to obtain leaf venation network images (Fig. 1). The detailed steps of the method of extracting leaf vein images used can be found in Yu & Liu (2021).

Image processing and data acquisition: Firstly, we scanned the leaves with an Epson scanner (V550, Epson, Batam, Indonesia) at 600 dpi resolution. Secondly, we used Photoshop (version 9.0) to generate black and white images of leaf edges. Thirdly, we used MATLAB (version ≥ 2009a) to extract the planar coordinates of the leaf edge for each image based on the procedure developed by Shi *et al.*, (2018). Fourthly, we used R (version 4.0.2; R Core Team, 2020) to calculate leaf area, perimeter, length, and width using the planar coordinates extracted in the previous step on the basis of the R script developed by Shi *et al.*, (2018) and Su *et al.*, (2020).

Models and statistical analysis: We proposed a new leaf shape index, named the ellipticalness index (EI), as follows:

$$\text{EI} = \frac{A}{\pi/4\,LW} \qquad (1)$$

where A, L, and W represent leaf area, length, and width, respectively.

We also calculated the value of the leaf roundness index (RI) for each leaf for comparison with EI values. Tukey's honestly significant difference (HSD) test (Hsu, 1996) was used to test whether the values of either leaf shape index differed significantly ($p<0.05$) between each pair of the nine species studied.

Table 1. Leaf sampling information for the nine studied species of Magnoliaceae.

Species code	Latin name	Leaf growth type	Location	Coordinates	Sampling time
1	*Magnolia amoena* Cheng	Deciduous	NBG-MSYS	32°3'27"N, 118°49'56"E	9 Sep. 2019
2	*Magnolia denudata* Desr.	Deciduous	NFU Campus	32°4'43"N, 118°48'33"E	13 Sep. 2019
3	*Magnolia soulangeana* Soul.-Bod.	Deciduous	NBG-MSYS	32°3'29"N, 118°49'55"E	30 Jul. 2019
4	*Magnolia tomentosa* Thunb.	Deciduous	NBG-MSYS	32°3'28"N, 118°49'55"E	30 Jul. 2019
5	*Michelia cavaleriei* var. *platypetala* (Hand.-Mazz.) N. H. Xia	Evergreen	NFU Campus	32°4'48"N, 118°48'30"E	26 Aug. 2020
6	*Michelia chapensis* Dandy	Evergreen	NBG-MSYS	32°3'28"N, 118°49'55"E	25 Jul. 2020
7	*Michelia compressa* (Maxim.) Sarg. Gard. et For.	Evergreen	NBG-MSYS	32°3'28"N, 118°49'55"E	30 Jul. 2019
8	*Michelia figo* (Lour.) Spreng.	Evergreen	NFU Campus	32°4'46"N, 118°48'28"E	13 Sep. 2019
9	*Michelia maudiae* Dunn	Evergreen	NFU Campus	32°4'45"N, 118°48'25"E	31 Jul. 2020

Note: NBG-MSYS represents Nanjing Botanical Garden Mem. Sun Yat-sen. NFU Campus represents Nanjing Forestry University Campus
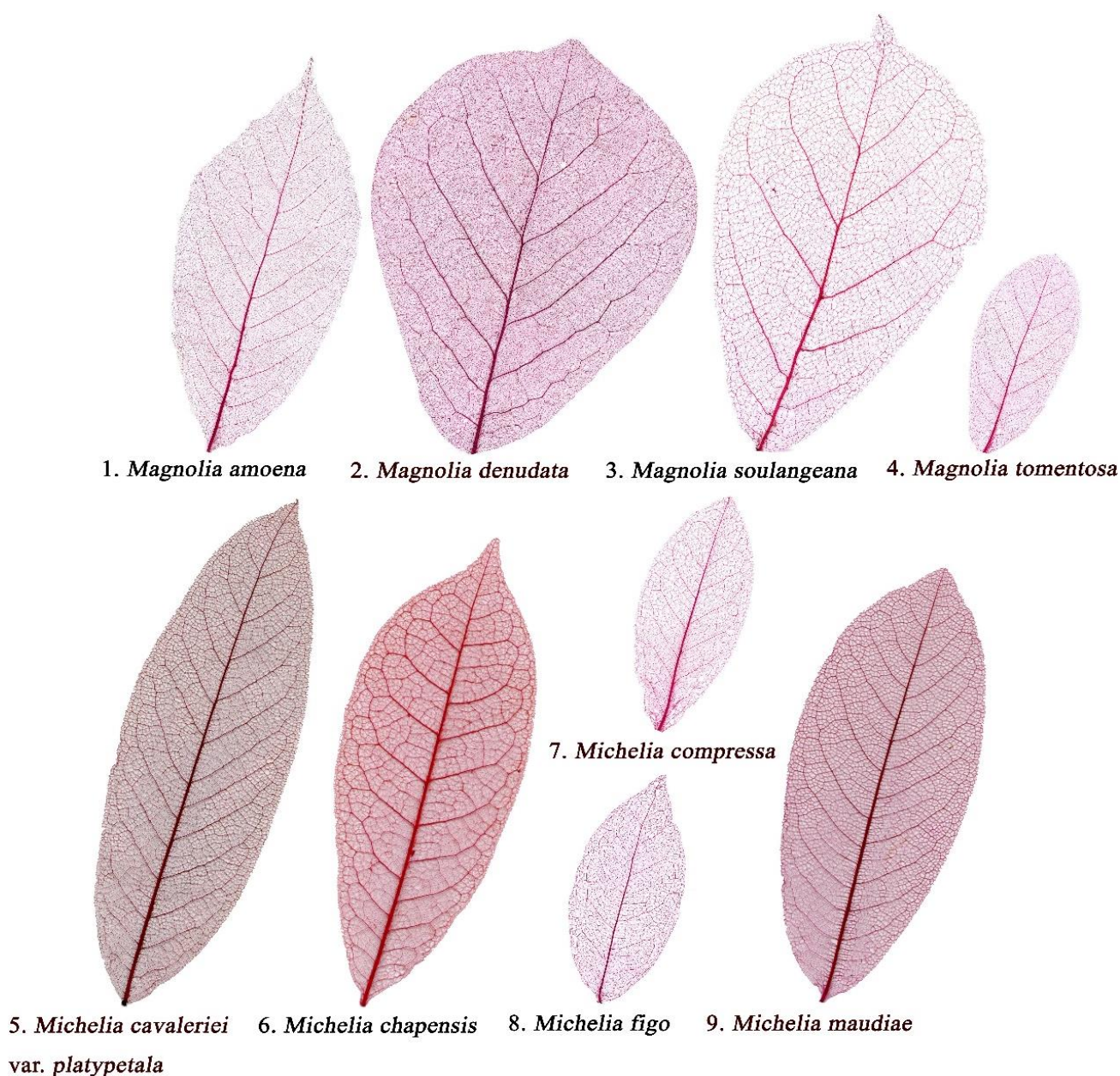
Fig. 1. Examples of chemically cleared leaves of the nine studied species of *Magnolia* and *Michelia*. The leaf veins were stained with 5% safranin solution for visualization (see Yu & Liu (2021) for details). The numbers before the species' Latin names are used as species codes hereinafter.

We also compared the Montgomery equation (ME), which predicts *A* as a proportional function of *LW*, with five other models of leaf area (Table 2; Shi *et al.*, 2019a). We did this because the Montgomery parameter (MP), which is the proportionality coefficient of the ME (i.e., $A = MP \times LW$), is closely associated with the EI in theory as follows:

$$EI = \frac{4}{\pi} MP \qquad (2)$$

To compare goodness of fit among the six leaf area models (Table 2), the root-mean-square error (RMSE) was used:

$$RMSE = \sqrt{\sum_{i=1}^{n} \left(A_i - \hat{A}_i\right)^2 \Big/ n} \qquad (3)$$

where *n* represents the number of leaves of a species examined, the subscript *i* represents the *i*-th leaf, and $\hat{A}$ represents the leaf area predicted by a model.

The absolute percent error (APE, in %) was calculated as follows:

$$APE_{ij} = \frac{\left|RMSE_j - RMSE_i\right|}{RMSE_i} \times 100\% \qquad (4)$$

and was used as a representation of the influence of an additional parameter on the goodness of fit achieved by a model (i.e., by how much increased model complexity improved model fit; Yu *et al.*, 2020).

Ordinary least-squares regression was used to estimate the parameters of the six tested leaf area models (Table 2). Model–2 in Table 2 can reflect the scaling relationship between the area of the planar projection of a leaf and a rectangle with leaf length and width as its sides. Provided that a leaf's surface is sufficiently flat, the numerical value of the scaling exponent of leaf projection area vs. the product of leaf length and width approximately equals unity (Shi *et al.*, 2019a). For Model-1, -3, and -5 in Table 2, there are fixed slopes of 1, 2, and 2 on a log-log plot. Log-log plots were used because the distribution of leaf area is usually slightly skewed, and so log-transformation helps to normalize the data (Shi *et al.*, 2019a; Yu *et al.*, 2020; Guo *et al.*, 2021). The bootstrap percentile method was used to calculate the 95% confidence interval (CI) of the difference in the estimated MP values between each pair of the nine studied species (Efron & Tibshirani, 1993; Sandhu *et al.*, 2011). If the 95% CI includes 0, this means there is no significant difference between groups, whereas if the 95% CI does not include 0, this means there is a significant difference.

All calculations and statistical analyses described above in this section were performed using R (version 4.0.2; R Core Team, 2020).

Results

The EI values ranged from 0.7 to 1.0 for the nine studied species of Magnoliaceae (Fig. 2A). This indicated that the leaf shapes of these nine species did not conform to a standard ellipse shape with leaf length (L) and width (W) as the major and minor axes. Among the nine species studied, *Magnolia tomentosa* and *Michelia maudiae* were found to have leaf shapes that most closely resembled a standard ellipse (Fig. 2A). However, their RI values were not the highest found, as *Magnolia denudata* had the roundest leaves (Fig. 2B). There was a significant correlation between EI and RI values ($r = 0.29$, $n = 2220$, $p<0.05$).

Among the six leaf area models tested, Model-2 had the lowest RMSE, and Model-1 (i.e., the ME) had approximately the same RMSE value as that of Model-2 for each species (Table 3). Although Model-1 has one more parameter than Model-2, the decrease in APE with Model-1 vs. -2 did not exceed 1.5% for any of the species of Magnoliaceae tested except *Magnolia soulangeana* (APE = 5.34%). This means that the additional parameter in Model-1 was apparently unnecessary for most species (8/9). The ME had a lower RMSE than those of the other four models that only include a linear leaf dimension (L or W). The estimated MPs ranged from 0.64 to 0.73 for all nine species, with RMSE values for the ME all being less than 0.05. In addition, the correlation coefficients between LW and A of the nine species as calculated on a log-log plot were all greater than 0.988 (Fig. 3). This showed that the ME achieved a good fit to the data of each tested species. The goodness of fit attained by the ME was still high even when the data of all nine species were pooled, resulting in an RMSE smaller than 0.05 and a high correlation coefficient of 0.9969 (Fig. 4). The estimated MP for the pooled data was 0.684, with the 95% CI encompassing values from 0.6827 to 0.6855. These results confirmed the validity of the ME for use in calculating leaf area. We carried out linear regressions of the estimated MP values vs. the mean EI values of the nine studied species, and the intercept was found to be non-significant ($p>0.05$). Therefore, we dropped the intercept term from the linear regression, and obtained a slope of 0.7850 (95% CI: 0.7848 to 0.7851) for the MP vs. EI relationship, which means that the MP is approximately equal to $\pi/4$ EI.

Table 2. The six models for calculating leaf area compared in this study.

Model No.	Model expression	Log-transformation of model
Model−1	$A = c(LW)$	$\ln(A) = a + \ln(LW)$
Model−2	$A = c_2(LW)^{b_2}$	$\ln(A) = a_2 + b_2 \ln(LW)$
Model−3	$A = c_3 L^2$	$\ln(A) = a_3 + 2\ln(L)$
Model−4	$A = c_4 L^{b_4}$	$\ln(A) = a_4 + b_4 \ln(L)$
Model−5	$A = c_5 W^2$	$\ln(A) = a_5 + 2\ln(W)$
Model−6	$A = c_6 W^{b_6}$	$\ln(A) = a_6 + b_6 \ln(W)$

Note: Model−1 is the Montgomery equation (ME), where $c = \exp(a)$. There are similar exponential relationships between the pre-exponential constants and the intercepts for the other models. Here, A denotes leaf area, L denotes leaf length, W denotes leaf width, and a and b (with different subscripts for different models) are constants to be estimated. In the actual fitting of data for each species, the log-transformed version of each model was used

Table 3. Root-mean-square error (RMSE) and absolute percent error (APE) values for the six tested leaf area models.

Species code	$RMSE_1$	$RMSE_2$	$RMSE_3$	$RMSE_4$	$RMSE_5$	$RMSE_6$	APE_{12}	APE_{34}	APE_{56}
1	0.0478	0.0477	0.1010	0.0964	0.0933	0.0933	0.28%	4.62%	0.03%
2	0.0384	0.0381	0.1028	0.0995	0.0679	0.0656	0.80%	3.28%	3.33%
3	0.0298	0.0282	0.0706	0.0674	0.0646	0.0622	5.34%	4.54%	3.64%
4	0.0309	0.0309	0.0733	0.0702	0.0784	0.0781	0.00%	4.26%	0.31%
5	0.0273	0.0273	0.1359	0.1178	0.1325	0.1259	0.07%	13.37%	4.94%
6	0.0298	0.0296	0.0861	0.0826	0.0732	0.0732	0.71%	4.11%	0.10%
7	0.0317	0.0317	0.0883	0.0801	0.0834	0.0830	0.15%	9.19%	0.48%
8	0.0309	0.0305	0.0925	0.0799	0.0693	0.0680	1.36%	13.69%	1.89%
9	0.0305	0.0304	0.1489	0.1294	0.1220	0.1218	0.62%	13.07%	0.16%

Note: The subscripts 1−6 of RMSE and APE in the first row represent the six leaf area models listed in Table 2
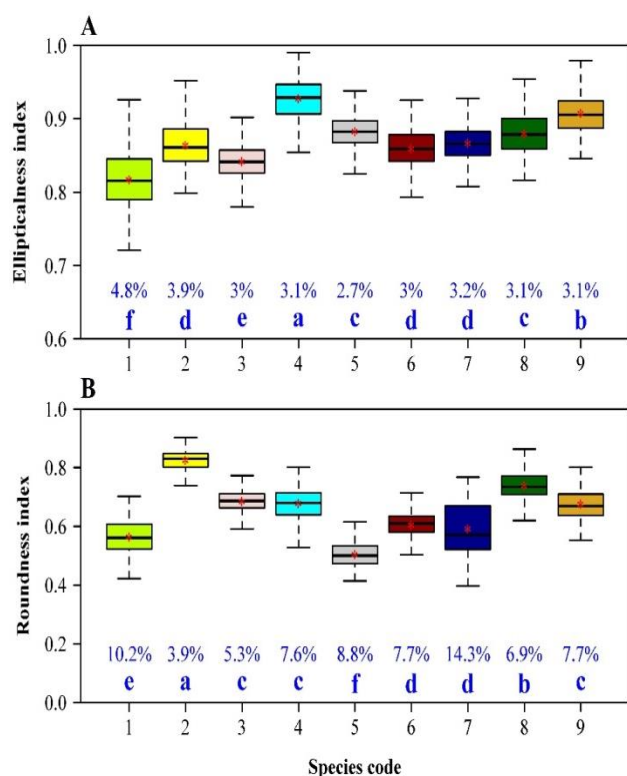
Fig. 2. Comparisons of the leaf ellipticalness (**A**) and roundness indices (**B**) among the nine species of Magnoliaceae studied. Different colors represent different species. Different lowercase letters represent species whose leaf shape index values were significantly different (Tukey's HSD test, $p<0.05$), and the alphabetical ordering of the letters used reflects the highest (a) to the lowest (f) mean leaf shape index value. The percentages above these letters are the coefficients of variation of the leaf shape index for each of the nine species. The red asterisk within a box represents the mean, and the horizontal solid line within a box represents the median.

Discussion

Differences and connections between the leaf ellipticalness index and Montgomery parameter: In the present study, we proposed a new leaf shape index, the leaf ellipticalness index (EI), which is closely related to the MP from the Montgomery equation. However, the geometrical meanings of these two measures are different. The EI is used to quantify the deviation of an oval leaf's shape from a standard ellipse with leaf L and W as the major and minor axes, while the MP is used to compute the proportion of the area of a rectangle with leaf L and W as its two side lengths represented by the area of a leaf. The MP has been demonstrated to apply to different leaf shapes, including leaves with many marginal teeth, serrations, dissections, and lobes (Shi *et al.*, 2019a,b; Yu *et al.*, 2020; Schrader *et al.*, 2021), but the EI appears to be more meaningful for plants with oval rather than other leaf shapes. Essentially, the MP is a correction factor allowing one to obtain different shapes from a rectangle, whereas the EI is a correction factor for obtaining different shapes from an ellipse. Whether both indices are valid depends on whether the ME is valid for the calculation of leaf A – i.e., whether A is proportional to LW. If this hypothesized proportionality holds true, the

MP estimate tends to be robust, with a narrow 95% CI. Correspondingly, the resulting estimate of the quotient of A (which is proportional to LW) and $\pi/4$ LW (i.e., EI) is robust. From the perspective of data-fitting, the robustness and processes involved in the estimation of the parameters of the MP and EI are the same.

Comparison of the leaf ellipticalness index with the leaf roundness and leaf dissection indices: The leaf roundness index (RI) has long been regarded as a measure of the deviation of leaf shape from a standard circle (Niinemets, 1998; Peppe *et al.*, 2011). It is effective for approximately round leaves. However, many leaf shapes are apparently different from a circle. In our results, eight out of nine species had mean RI values less than 0.8 (Fig. 2B). However, all species had mean EI values greater than 0.8 (Fig. 2A). When leaf L and W are the same, then in theory RI = EI. However, for a leaf shape that deviates from a standard circle to a certain degree, the two indices are not the same (Figure 2A vs. 2B) because the bases of their calculation are different. For a standard circle, $A = \pi r^2$ and $P = 2\pi r$, so it is easy to express A as a function of P, or to express P as a function of A. The leaf RI is based on the ratio of $4\pi A$ to P^2, so in theory it has a constant value of one for a standard circle. If a leaf shape deviates from a circle, the actual leaf P is usually larger than the perimeter of a circle, and as a result RI < 1. The EI is calculated based on the ratio of leaf area to the hypothesized area of an ellipse with comparable axes; the formula to calculate the area of an ellipse is well-known, $\pi\alpha\beta$, with α being the semi-major axis and β the semi-minor axis of the ellipse (related directly to W and L in the rectangle of the ME). It is difficult to analytically express leaf A or P as a function of one another (Almkvist & Berndt, 1988). Thus, it is impossible to provide a candidate ellipticalness index based on the ratio of leaf P^2 to A. Nevertheless, it is still somewhat meaningful to use a leaf shape index based on these two leaf measures, such as the leaf P/A ratio or the leaf P^2/A ratio, to reflect the complexity of leaf shape regardless of the extent to which leaf shape deviates from a standard ellipse.

The leaf dissection index (DI; Kincaid & Schneider, 1983; Thomas & Bazzaz, 1996; Santiago & Kim, 2009) is used to describe the complexity of leaf shape, especially the influence of marginal teeth, serrations, dissections, and lobes on leaf perimeter. However, the leaf DI is actually the square root of the reciprocal of the leaf RI. The DI itself cannot completely qualify the extent to which marginal teeth, serrations, dissections, and lobes affect leaf shape. This is because the leaf W/L ratio (deviating from an ideal 1:1 ratio of a hypothesized standard circle for complex leaf shapes) and the degree to which the leaf edge deviates from being a smooth line can both affect the DI value. Our EI also cannot describe the extent of leaf marginal dissection because the EI is based on an area: area ratio, without leaf perimeter being involved in its calculation. To reflect the extent of leaf marginal dissection (i.e., deviation from smoothness), we suggest first using a parametric or a non-parametric model to describe the leaf profile. Then, one could use the leaf P/A ratio to reflect leaf shape complexity, especially that resulting from leaf marginal teeth,

serrations, dissections, and lobes. For example, the simplified Gielis equation can describe many bilaterally symmetrical leaf shapes despite the fact that it does not accurately fit the leaf margins for some leaves (Gielis, 2003; Shi *et al.*, 2015, 2018). If a leaf is exactly or approximately bilaterally symmetrical, but with some teeth, dissections, serrations, or lobes, then the *P/A* ratio is likely sufficient to reflect the extent of deviation of the leaf margin from smoothness. If a leaf slightly deviates from perfect bilateral symmetry, one can use a coordinate transformation based on the method proposed by Huang *et al.*, (2020) to make the simplified Gielis

equation reflect the deviation of the leaf edge from bilateral symmetry. Then, the *P/A* ratio could be used to quantify the deviation of the leaf margin from smoothness. Because a clear polar coordinate equation is available in this case, it is easy to calculate the perimeter and area of the curve generated by the polar coordinate equation. In this case, we could further quantify the extent of leaf margin deviation from smoothness for a leaf separately from the influence of leaf shape, especially that of the leaf *W/L* ratio and that of a skewed leaf marginal curve.
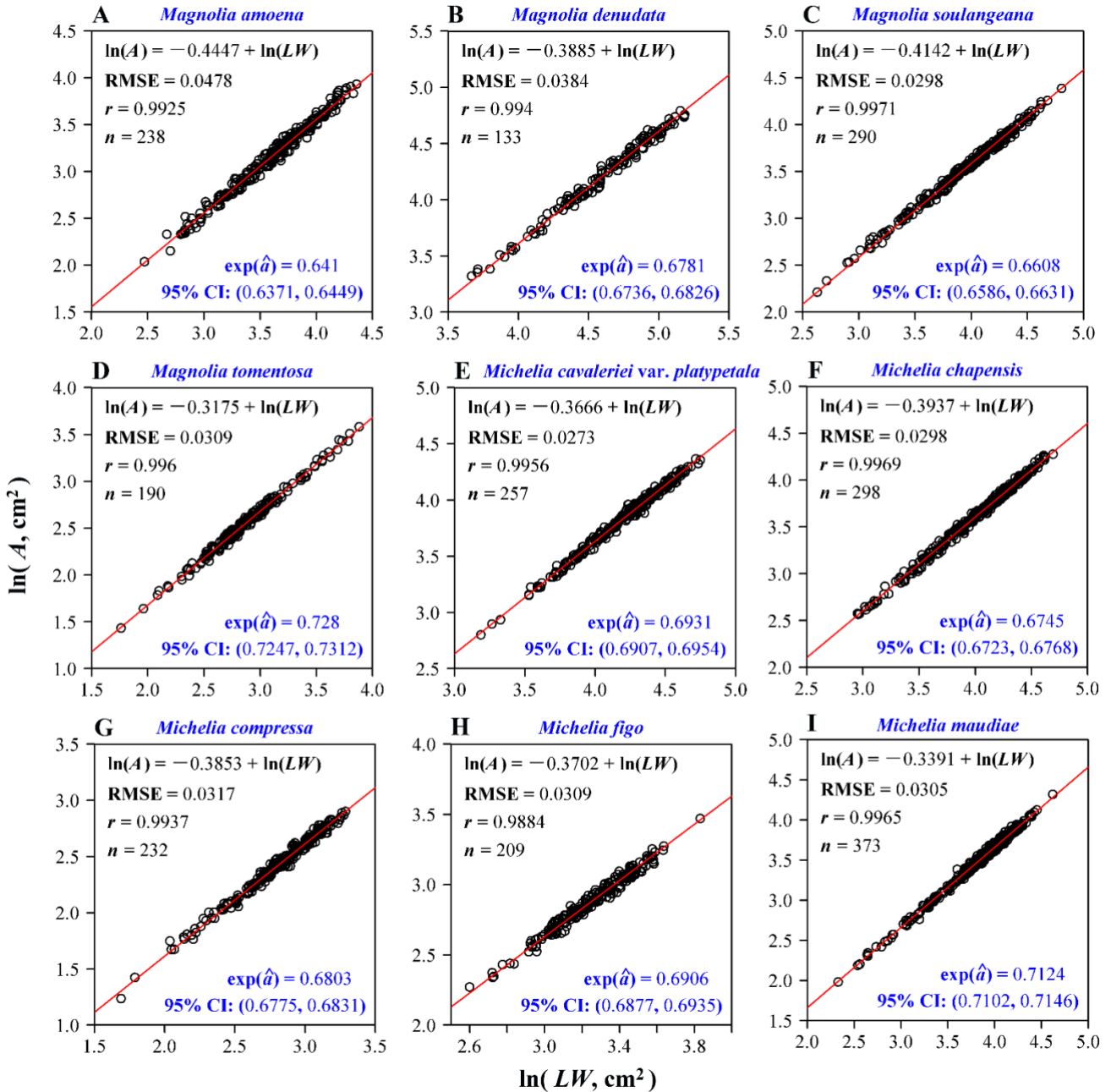

Fig. 3. Results of fitting the Montgomery equation to the data for individual species, represented as log-log plots of leaf area (*A*) vs. the product of leaf length (*L*) and width (*W*). Here, 'ln' represents the natural logarithm, RMSE represents the root-mean-square error of a linear fit, *r* represents the Pearson's linear correlation coefficient calculated between *A* and *LW* on each log-log plot, *n* represents the sample size (i.e., the number of leaves examined for each species), $\exp(\hat{a})$ represents the estimated Montgomery parameter, and 95% CI represents the 95% confidence interval of each Montgomery parameter estimate. Panels (**A**−**I**) represent the fitted results for different species. In each panel, small open circles represent the raw data, and the red straight line represents the linear regression line (with slope = 1) calculated for these data based on the ordinary least-squares method.
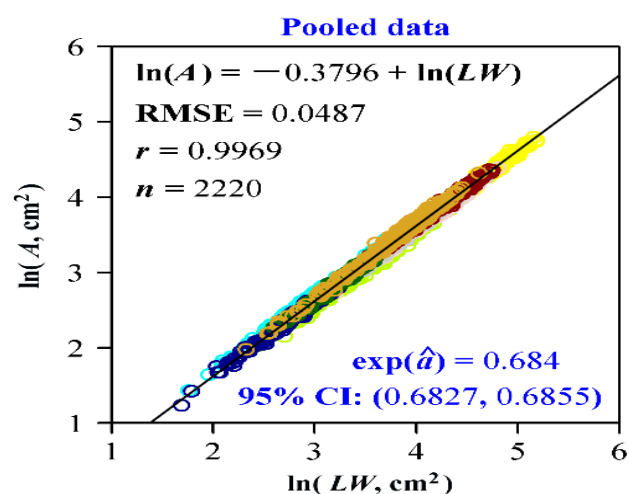
Pooled data

$\ln(A) = -0.3796 + \ln(LW)$

RMSE $= 0.0487$

$r = 0.9969$

$n = 2220$

$\exp(\hat{a}) = 0.684$

95% CI: (0.6827, 0.6855)

Fig. 4. Results of fitting the Montgomery equation to the pooled data of all nine species, represented as a log-log plot of leaf area (A) vs. the product of leaf length (L) and width (W). Here, 'ln' represents the natural logarithm, RMSE represents the root-mean-square error of a linear fit, r represents the Pearson's linear correlation coefficient calculated between A and LW on a log-log plot, n represents the sample size (i.e., the total number of leaves sampled for all nine species), $\exp(\hat{a})$ represents the estimated Montgomery parameter, 95% CI represents a 95% confidence interval of the Montgomery parameter estimate, small open circles represent the raw data, and the red straight line represents the linear regression line (with slope = 1) calculated for these data based on the ordinary least-squares method.

Conclusions

In this study, we proposed a new leaf shape index (i.e., the ellipticalness index, EI) that can measure the extent to which an oval leaf shape deviates from a standard ellipse. This index is not an extension of the leaf roundness index (RI), because the bases of modelling the two leaf shape indices are different. The EI is based on the proportional relationship between leaf area (A) and the product of leaf length (L) and width (W), while the RI is based on the fact that the leaf perimeter (P) squared is proportional to leaf A. For the RI or its rewritten form, the leaf dissection index (DI), the influence of leaf shape (reflected by the leaf W/L ratio or by a skewed leaf marginal curve along the axis from the leaf base to the leaf apex) on the index value cannot be separated from those of leaf marginal teeth, serrations, dissections, and lobes. For instance, for oval leaves with dissections (e.g., some Rosaceae; Yu *et al.*, 2019), the contribution of the W/L ratio or that of a skewed leaf marginal curve (from leaf base to leaf apex) to the RI might be larger than that of unsmooth leaf margins. Unlike the RI, the newly developed EI can be applied to both circular and oval leaves. We also checked whether the Montgomery equation (ME) holds true for nine species of Magnoliaceae. We found that the ME can fit the leaf area data well for each of these species (considering that all RMSEs were smaller than 0.05 and all correlation coefficients were greater than 0.988), and this demonstrated the validity of the ME's use in describing the relationship between leaf A and LW. The formula for the area of an ellipse is $A = \pi\alpha\beta$, where α and β are the semi-major and semi-minor axes of the ellipse, and these are one half each of

a leaf's L and W, respectively. Thus, whether the EI provides a robust fit to leaf shape data depends on whether the relationship between A and LW can be fit well by the ME. The EI is actually proportional to the proportionality coefficient in the ME (i.e., the Montgomery parameter, MP). However, the MP only calculates the proportion of the area of a rectangle with leaf L and W as its two side lengths represented by the actual leaf A, and does not intuitively reflect the deviation of a leaf's shape from a standard ellipse. In addition, we also compared the ME with five other models of leaf area, and found that the ME was the best one based on consideration of the trade-off between the goodness of fit achieved and model complexity. This study provides a useful tool for quantifying and comparing the oval leaf shapes that render leaf hydraulic conductance to be homogeneous across the whole leaf surface.

Using the RI and EI, no instances are found where RI = 1 or EI = 1. This means that neither circles, nor true ellipses are found in nature, which is in accord with the findings in past studies of bamboo culms, tree rings, and leaves (Gielis *et al.*, 2021). However, the RI and EI allow us to quantify deviations from ideal circles and ellipses, which forms a basis for using the language of mathematics to study some special natural shapes. Our results provide further qualitative and quantitative evidence that nature is inherently anisotropic, and new mathematical methods need to be developed to fully account for this, certainly in botany.

Acknowledgments

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