Universiteit Antwerpen

This item is the archived peer-reviewed author-version of:

A generalized performance equation and its application in measuring the Gini index of leaf size inequality

Reference:
Lian Meng, Shi Peijian, Zhang Liuyue, Yao Weihao, Gielis Johan, Niklas Karl J..- A generalized performance equation and its application in measuring the Gini index of leaf size inequality
Trees: structure and function - ISSN 1432-2285 - 37(2023), p. 1555-1565
Full text (Publisher's DOI): https://doi.org/10.1007/S00468-023-02448-8
To cite this reference: https://hdl.handle.net/10067/1995620151162165141

uantwerpen.be
Institutional repository IRUA

A generalized performance equation and its application in measuring Gini index of leaf size

Meng Lian[1,2], Karl J. Niklas[2], Liuyue Zhang[1,4], Weihao Yao[2], Johan Gielis[5], Peijian Shi[1,2]

[1] Department of Applied Mathematics, College of Science, Nanjing Forestry University, Nanjing 210037, People's Republic of China

[2] Bamboo Research Institute, College of Ecology and Environment, Nanjing Forestry University, Nanjing 210037, People's Republic of China

[3] Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, USA

[4] Key Laboratory of Bio-Resource and Eco-Environment of Ministry of Education, College of Life Sciences, Sichuan University, 29 Wangjiang Road, Chengdu 610064, People's Republic of China

[5] Department of Biosciences Engineering, University of Antwerp, B‐2020 Antwerp, Belgium

Correspondence:

Peijian Shi, PhD

pjshi@njfu.edu.cn

Running title: **Measure of leaf size inequality**

Abstract

The performance equation is used to describe the effect of temperature on the behavioral performance of animals, which can produce flexible asymmetrical and symmetrical bell-shaped curves. The Lorenz curve (accumulative proportion of household income vs. accumulative proportion of households) is a basis for calculating the Gini index which measures the inequality of household income. There is a certain variation in leaf-size distribution for one plant which gauges the adaptation of the plant to inter- and intra-specific competition and environments. The Gini index can be used to quantify such an inequality of leaf-size distribution. In the present study, we sampled 12 individual plants for a dwarf bamboo, and measured the area and dry mass for every leaf on each of 12 plants. We proposed a generalized performance equation (GPE) that can regard the traditional performance equation (PE) as its one special case, and fitted the Lorenz curve of leaf size rotated anticlockwise by −135° using GPE and PE, respectively. We found that GPE is better than PE in fitting the Lorenz curve from the trade-off between model structural complexity and goodness of fit. We compared the Gini index of leaf area with that of leaf dry mass, and found that there was a significant difference between the two indices which might result from the allometric relationship between leaf dry mass and area. Nevertheless, there was a strong correlation between the two Gini indices (r = 0.99). The present study provides a promising tool for quantifying the inequality of leaf size distribution across individual plants and serving as a reference trait for reflecting the adaptation of plants to environments.

Keywords: Inequality of leaf size distribution; Gini index; Model comparison; Performance equation; *Shibataea chinensis*

Introduction

Photosynthesis is at the basis of life, and photosynthetic organisms have developed a variety of forms and shapes to capture sunlight, both in their constructional organisation and the shape of their photosynthetic organs. Plants have developed, in response to environmental challenges, a variety of growth forms, ranging from herbs and annuals, shrubs and trees, to a metamorphosis of stems and leaves into succulent forms, or into plagiotropically growing rhizomes in grasses and bamboos. The constructional organization is that of an iteration of metamers or phytomers, constructional units consisting of a part of the stem, consisting of a node and the leaf at that node, with a bud subtended at that node if present. Whereas the leaves can take on many forms, in the case of photosynthesis, it is foliage leaves which are the main photosynthetic organs of plants. They can be connected directly to the node, or via a petiole. In the case of grasses and bamboo, the culm sheath connects to the node, and via a shoulder (e.g. in corn) or via a pseudo-petiole (in bamboos), the foliage leaf is connected to the culm sheath. A major question is the variation of size and form of foliage leaves within one plant.

heeft verwijderd: Foliage leaves are

heeft verwijderd: s.

Leaf distribution patterns closely match with the above-ground architectural structure of plants (Küppers 1989). Trees can display different crown geometries, including broad, columnar, fortunate, layered, oval, pyramidal, round, shrubby, vase, and weeping crowns, etc. The inter- and intra-specific competition of plants can significantly affects the growth and orientation of branches and leaves (Sumida et al. 2002). The branch positions of leaf growth on a plant, resulting in the heterogeneity of light intercept, can influence leaf size and shape (Bruschi et al. 2003). In general, newly emerging leaves are located at the outside of the crown, and are smaller than older leaves. Sun leaves are larger and thinner, shade leaves are smaller and thicker, and the two types of leaves have a difference in shade tolerance that can be reflected by leaf dry mass per unit leaf area (Poorter et al. 2009; de Casas et al. 2011). In addition, the difference of leaf growing positions for intercepting light can cause the leaf bilateral asymmetry of leaves to a degree (Wang et al., 2018). The distribution of leaf size can reflect the influence of

heeft verwijderd: here are

the fractal dimension of branches (i.e., the aboveground architectural structure), which are closely related to plant strategies (Küppers 1989). Thus, it is important to explore the leaf size distribution patterns. Leaf area and leaf dry mass both can represent leaf size, but their relationship is not isometric, which has been confirmed for many plant groups (Milla and Reich, 2007; Niklas et al. 2007). The increase of leaf area doesn't keep pace with that of leaf mass. However, the two leaf-size measures have a robust power-law relationship, and keep a significant positive correlation on a log-log scale. Whether the variation of leaf area per plant is the same as or similar to that of leaf mass has not been tested by prior studies. In fact, there are few studies that have quantified the variation of leaf size in the same plant apart from few studies (e.g. Shi et al. 2015), probably because there are too much leaves on a woody plant. It is time-consuming to count all leaves for a woody plant especially trees. To sample all leaves is infeasible for many protected precious tree species. For herbaceous plants, the number of leaves are too small or it is difficult to separate leaves from the stalk given the lack of leaf petiole. In addition, the leaves for many herbaceous plants are not sufficiently flat to obtain their area. It leads to a quantitative difficulty in measuring the inequality of leaf size distribution per plant. One strategy of assessing inequality is the Gini coeffient, based on the Lorenz curve.

The Lorenz curve is widely used to study the inequality of household income (Lorenz 1905; Gastwirth 1971). It is the curve of the accumulative proportion (or represented by percentage) of household income plotted against the accumulative proportion of households. If the household income distribution is absolutely equal, the Lorenz curve overlaps with the straight line of $y = x$; if the extent of inequality is large, the Lorenz curve tends to protrude towards the (1, 0) point in the plane (Figure 1a). The Gini index is equal to the ratio of the area encircled by the straight line of $y = x$ and the Lorenz curve to 0.5 (i.e., the triangular area formed by the straight line of $y = x$ with $x = 1$ and $y = 0$). When the Gini index equals 1, it represents an absolute inequality in household income distribution; when the Gini index equals 0, it represents an absolute equality in household income distribution. The Gini coefficient is a common metric used to compare the income inequality among different countries

heeft verwijderd: .

(https://data.oecd.org/inequality/income-inequality.htm).

This concept has been applied to many other study areas apart from economics, e.g., (Tanikawa et al. 2012; Wang et al. 2012; Chen et al. 2016). In botany, there are some studies using the Lorenz curve and Gini coefficient to measure inequality of plant size and seed size (Hara 1986; Taylor and Aarssen 1989; Metsaranta and Lieffers 2008; Chen et al. 2014). However, there is no study to apply the Gini index to quantify the variation in leaf size of plants. In addition, the predictor and response variable of the Lorenz curve are accumulative, which means that the datum in the Lorenz curve is the sum of the previous data (Figure 1a). This usually leads to the auto-correlation, and requires using the maximum likelihood method to estimate the parameters of the equations describing the Lorenz curve (referred to as Lorenz equations hereinafter). The validity of the maximum likelihood method seriously depends on the model structural complexity (Chotikapanich and Griffiths 2002). For a complex Lorenz equation, the maximum likelihood method tends to fail to obtain the target parameters in a global optimization fashion.

We further note that the Lorenz curve exhibits a left-skewed bell-shaped curve when being rotated anticlockwise by −135° around the origin point (Figure 1a,b). The shape of the rotated Lorenz curve is very similar to the temperature-dependent performance curve of animals (Huey 1979). A temperature-dependent performance equation that was early proposed to describe the effect of temperature on the jumping distance of frogs has been found to be applicable to describe the effect of temperature on other behavioral performance such as development rate of arthropods (Shi et al. 2011; Wang et al. 2013). When replacing temperature with growth time, the performance equation and other similar equations can be regarded as a growth rate equation (i.e., the derivative of a sigmoid growth equation) and its integral can produce a sigmoid equation (Shi et al. 2017, 2022). Relative to the absolute equality line of income distribution (i.e., $y = x$), the rotated Lorenz curve exactly can be deemed as a 'growth rate' curve. In this way, we can use an existing performance equation to fit the rotated Lorenz curve so that the auto-correlation of data can be weakened to a large degree. In

addition, we need to note that to directly fit the original Lorenz curve, the prediction errors cannot be easily observed because the accumulation of household income tends to hide the residuals between the observations and the predicted curve (Figure 1a); however, using the rotated observations and Lorenz curve, the predictor errors are easier showed (Figure 1b). Finally, such a rotation is more reasonable according to the definition of the Lorenz curve for calculating the Gini index that should be mainly used to measure the extent of deviation from the 45° straight line in the unit square (Figure 1a). The rotated Lorenz curve exactly directly reflect the deviation from the 45° straight line being rotated as the horizontal axis (Figure 1b).

To test whether the performance equation or its generalized version (that is about to be proposed below) can well describe the rotated Lorenz curve of leaf size, we need to use a plant that has a limited number of leaves whose area can be measured in a simple manner. Dwarf bamboo is an ideal material, because the number of leaves are not too much and the leaves have false petioles (that are very short). In the present study, we used 12 individual plants of *Shibataea chinensis* Nakai, a native dwarf bamboo growing in southern China that usually have 10 to 40 leaves per plant, and the leaves are relatively flat (Figure 2). A notable feature of *Shibataea sinensis* is the relatively low variation in leaf shape and length (Lin et al.)

heeft opmaak toegepast: Lettertype: Cursief

Note From **Testing bilateral symmetry of bamboo leaf using simplified Gielis equation;** upper row: leaf length, lower row Shape parameter

Met opmaak: Uitvullen, Rechts: 1,64 cm, Regelafstand: 1,5 regel, Zwevende begin- en eindregels niet voorkomen, Spatiëring tussen Aziatische en Latijnse tekst aanpassen, Spatiëring tussen Aziatische tekst en nummers aanpassen, Tabstops: 14,64 cm, Left + 14,75 cm, Left

heeft opmaak toegepast: Lettertype: (Standaard) +Hoofdtekst (Calibri), 11 pt, Engels (V.S.)

heeft opmaak toegepast: Engels (V.S.)

Sh. Sinensis 41	Mean 9.00	Median 8.70	Standard error 1.82	
Sh. Sinensis41	Mean 0.0858	Standard erro 0.0039	30	a

We measured the area of and dry mass for each leaf, and used the performance equation and its generalized version to fit the accumulative proportion of leaf size vs.

that of leaves rotated anticlockwise by −135° around the origin point. We tested whether the Gini index of leaf area was equal to or correlated to the Gini index of leaf dry mass. This will provide a useful tool for calculating the inequality of leaf-size distribution. If the two types of Gini indices are the same or strongly correlated, we can use the Gini index of leaf area rather than that of leaf dry mass. Because leaf area is demonstrated to be proportional to the product of leaf length and width for many broad-leaved plants with different leaf shapes, we can non-destructively measure leaf area than using leaf dry mass that is involved in destructive sampling. Here, we tested the validities of two performance equations in fitting the observations of leaf size, and tested whether the Gini index of leaf area is the same as or correlated to that of leaf dry mass.

Materials and methods

Leaf sampling

We randomly sampled 12 individual plants of *S. chinensis* growing in Nanjing Forestry University campus (118°48′53″E, 32°4′52″N), Nanjing, China in early October, 2022. The aboveground part of each individual plant was obtained by cutting the stalk along the ground (Figure 2), which was then wrapped by wet newspaper and taken back to the lab within one hour.

heeft verwijderd: '

heeft verwijderd: '

heeft verwijderd: '

heeft verwijderd: '

heeft verwijderd: '

heeft verwijderd: '

Data acquisition

The leaves were cut from the branches and the pseudo-petioles were removed. Each leaf was scanned by a photo scanner (V550, Epson, Batam, Indonesia) at a resolution of 600 dpi and saved as a .jpg file. And the .jpg files were converted into black-white images after being cropped and saved as .bmp format using Adobe Photoshop CS2 (version 9.0; Adobe, San Jose, CA, USA). The MATLAB (version ≥ 2009a; MathWorks, Natick, MA, USA) with a function developed by Shi et al. (2015, 2018) were used to extract the planar boundary coordinates of each leaf. We used the 'bilat' function in the 'biogeom' package (version 1.0.5; Shi et al. 2022a) based on R (version 4.2.0; R Core Team 2022) to calculate leaf area, length and width. Envelopes containing leaves were placed into a ventilated oven (XMTD–8222; Jinghong Experimental Equipment Co.,

Ltd., Shanghai, China) at 80°C for at least 72 h. The dry mass of each leaf was determined using an electronic balance (ME204/02, Mettler Toledo Company, Greifensee, Switzerland; measurement accuracy 0.0001 g). The raw data of leaf length (L), width (W), area (A) and dry mass (M) for all leaves of the 12 individual plants can be assessable from Table S1 in the online supplementary data.

The data of the accumulative proportion of A vs. the accumulative proportion of number of leaves per plant for each of the 12 individual plants were then obtained. The data were being rotated anticlockwise by −135° around the origin point and then were removed (rescaled to the) right by a distance of $\sqrt{2}$ (Figure 3a).

Performance equations

The original performance equation (PE; Huey 1979; Shi et al. 2011) was used

$$y = c\left(1 - e^{-K_1(x-x_1)}\right)\left(1 - e^{K_2(x-x_2)}\right) \quad (1)$$

Here, y represents the vertical distance of an arbitrary point on the Lorenz curve to the rotated 45° straight line (Figure 3b), and x represents the horizontal coordinate of the associated point on the rotated 45° straight line; c, K_1, K_2, x_1 and x_2 are parameters to be estimated, among which x_1 and x_2 represent the lower and upper intersect points of the performance curve with the x-axis. It is apparent that $x_1 = 0$, and $x_2 = \sqrt{2}$ for the rotated Lorenz curve (Figure 3b). This means that equation (1) can be simplified to a three-parameter model. In the present study, we introduced two additional parameters, a and b, to equation (1) to increase the flexibility of the curve in data fitting:

$$y = c\left(1 - e^{-K_1(x-x_1)}\right)^a \left(1 - e^{K_2(x-x_2)}\right)^b \quad (2)$$

We refer to equation (2) as the generalized performance equation (GPE) hereinafter. Note that in the present study x_1 and x_2 are both known constants. We used PE and GEP to fit the rotated data of the accumulative proportion of A vs. that of number of leaves per plant, and the rotated data of the accumulative proportion of M vs. that of number of leaves per plant, respectively.

Parameter estimation and model selection for the two performance equations

To estimate the parameters of PE and GPE, the residual sum of squares (RSS) between the observed and predicted *y*-values were minimized using the Nelder-Mead optimization algorithm (Nelder and Mead 1965), which was carried out using the 'IPEC' package (version 1.0.3; Shi et al. 2022b) based on R (version 4.2.0; R Core Team 2022).

The Akaike information criterion (AIC) was used to compare the performance equations (i.e., PE and GPE), and this criterion reflects the trade-off between the goodness of fit and model structural complexity. The equation with a lower AIC was regarded as the better one.

Calculation and comparison of the Gini indices of leaf area and dry mass

According to the definition of the Gini index, we can obtain it according to the estimated PE or the estimated GPE as follows:

$$\text{Gini index} = \frac{1}{2} - \int_0^{\sqrt{2}} f(x)\,dx \tag{3}$$

where $f(x)$ is PE or GPE. We used the one with a lower AIC on between PE and GPE to calculate the Gini index of A and that of M. Then we used the paired *t*-test to test the significance of the difference between the two types of Gini indices.

Scaling relationship between leaf dry mass and leaf area

To check whether the Gini coefficient of A is equal to that of M for each individual plant, we need to check whether M is proportional to A. We analyzed the scaling relationship between M and A:

$$M = \beta A^{\alpha} \tag{4}$$

Here, β is the normalized constant, and α is the scaling exponent. If $\alpha = 1$, M and A have a proportional relationship; otherwise, there is an allometric relationship indicating that the increase of A does not keep pack with that of M. The log-transformation was used on the two sides of equation (4) to stabilize the variance (Niklas 1994):

$$Y = \gamma + \beta X \tag{5}$$

where $Y = \ln(M)$, $X = \ln(A)$, and $\gamma = \ln(\beta)$. The reduced major axis was used to estimate the intercept and slope (Niklas 1994; Quinn and Keough 2002). The bootstrap percentile method (Efron and Tibshirani 1993; Sandhu et al. 2011) was used to calculate the 95% confidence interval (CI) of the slope of M vs. A.

Results

The original performance equation (PE) and its generalized version (GPE) both fit the data of the accumulative proportion of A vs. that of number of leaves per plants, and the data of the accumulative proportion of M vs. that of number of leaves per plants well, and all coefficients of determination (i.e., r^2) were greater than 0.99. However, GPE performed better overall. For 10 out the 12 individual plants, the AIC values of GPE were lower than those of PE in the inequality measure of A distribution (Figure 4); for 11 out of the 12 individual plants, the AIC values of GPE were lower than those of PE in the inequality measure of M distribution (Figure 5). For the inequality measure of A distribution, the Gini indices ranged from 0.0551 to 0.1834 (Figure 4); for the inequality measure of M distribution, the Gini indices ranged from 0.0704 to 0.1891 (Figure 5). There was a significant correlation between the two types of Gini indices ($r = 0.9923$, and $P < 0.001$; Figure 6). However, there was a significant difference between the two types of Gini indices based on the paired t-test ($t = -3.40$, $df = 11$, and $P = 0.0059 < 0.05$).

There is a significant scaling relationship between M and A given that the 98% CI of the slope of M vs. A on a log-log scale did not include zero (Figure 7). Because the lower bound of the 95% CI of the scaling exponent equaled $1.055 > 1$, it confirmed the hypothesis of diminishing returns of leaves, i.e., the increase of A tends to decrease with per unit M increasing (Niklas et al. 2007).

Discussion

Here, we mainly discussed the reasons for the strong correlation between the Gini index for the inequality measures of A and M, respectively, and for the significant difference between the two types of Gini indices. Additionally, we compared a possibility of

heeft verwijderd: *A*

heeft verwijderd: and that for *M* inequality measure

calculating the Gini index of leaf size distribution based on a non-destructively sampling method.

Reason of the difference in the two types of Gini indices

Assume that M is proportional to A, $M = \beta A$, where β is a proportionality coefficient. The accumulative proportion of M is equal to

$$\frac{\sum_{i=1}^{n_1} M_i}{\sum_{i=1}^{n} M_i} = \frac{\sum_{i=1}^{n_1} \beta A_i}{\sum_{i=1}^{n} \beta A_i} = \frac{\sum_{i=1}^{n_1} A_i}{\sum_{i=1}^{n} A_i} \quad (6)$$

where n_1 represents an arbitrary number of leaves which is smaller than the total of leaves (n) of a plant. We can find that the accumulative proportion of M is the same as that of A under the hypothesis of the proportional relationship between M and A. However, this hypothesis does not hold true for many plant groups (Milla and Reich, 2007; Niklas et al. 2007; Huang et al. 2020). Huang et al. (2020) examined the scaling relationships of leaf dry mass of 101 bamboo taxa, including species, cultivars, forms and varieties, and found that for 83 out of the 101 bamboo taxa (i.e., 82.2%) the lower bounds of the 95% CIs of the scaling exponents of M vs. A were greater than unity, which demonstrated that the proportional relationship between M and A did not hold true. Due to the allometric relationship between the two leaf size measures, given that the horizontal variables are both the accumulative proportion of number of leaves per plant for the Lorenz curve, it caused the significant difference between the types of Gini indices.

Strengths of the Gini index for leaf area distribution

Because of the strong correlation between the Gini index of A distribution and that of M distribution, in practice we could select any one to quantify the inequality measure of leaf size. However, to use leaf dry mass or leaf fresh mass, it is necessary to nondestructively sample leaves from the plant. In addition, to dry leaves is also a time-consuming work. Relative to leaf fresh or dry mass, A appears to be easily calculated via portable software or other non-destructive approaches for the estimation of leaf area (Schrader et al. 2017, 2021; Shi et al. 2019; Yu et al. 2020). In that case, we can calculate

heeft verwijderd: *en*

the Gini coefficient of A distribution by directly measuring the leaf length (L) and width (W). Here, we used the Montgomery equation assuming a proportional relationship between A and the product of L and W, to fit the data of A vs. LW in order to estimate the proportionality coefficient. Figure 8 shows that the numerical of the proportionality coefficient in the Montgomery equation was equal to 0.6399 with the 95% CI: 0.6363, 0.6436. According to 0.6399 LW, the predicted values of A were obtained. And then we calculated the Gini indices based on the predicted values of A, and compared them with those based on the observations of A using the paired t-test. We found that there was no significant difference between the two groups of Gini indices using the observed and predicted values of A (t = 1.8753, df = 11, and P = 0.0875 > 0.05). In practice, the calculation of leaf area can be further simplified to LW for the plants with similar leaf shapes or the plants in the same taxon (Shi et al. 2019; Baird et al. 2021). In that case, we even do need not destructively sample any leaves for examining the proportional relationship between A and LW.

Other temperature-dependent rate equations used for fitting the rotated Lorenz curve

In the present study, we mainly focused on a classical performance equation and its generalized version. However, there are many other temperature-dependent rate models that can produce different skewed bell-shaped curves (i.e., Ratkowsky et al. 1983; Yin et al. 1995; Lobry et al. 1991; Rosso et al. 1993; Brière et al. 1999; Shi et al. 2017; Jin et al. 2022). The reason that we chose the performance equation (Huey 1979; Shi et al. 2011) is the shape of the curve's left part that are convex upward, which exactly reflect the rotated data of the accumulative proportion of leaf size vs. that of number of leaves per plant for the studied bamboo species. However, for measuring the inequality of other study materials such as seed weight, plant biomass, given that the Lorenz curve can vary across those study materials, it is worthwhile to introduce other equations for calculating the Gini index, especially the modified Brière equation, the modified Yin equation, and the modified Lobry–Rosso-Flandrois equation (Jin et al. 2022; Shi et al. 2022). To do model comparison for different study materials appear to be valuable in future studies related to the study object of interest.

Conclusions

In the present study, the Lorenz curve was applied to calculate the Gini coefficient of leaf size per plant. The Lorenz curve rotated counterclockwise by −135°, and it could be described by the original performance equation, which was ever used to describe the temperature-dependent behavioral performance of animals, and its generalized version proposed here. The coefficient of determinations of the two performance equations for the rotated data of the proportional of leaf size (reflected by leaf area and leaf dry mass, respectively) vs. that of number of leaves per plant were greater than 0.99, which demonstrated the validities of the two performance equations. Nevertheless, the generalized version was better than the original version based on a lower AIC. The Gini indices calculated using the generalized performance equation ranged from 0.0551 to 0.1834 for the inequality measure in leaf area, and ranged from 0.0704 to 0.1891 for that in leaf dry mass for the 12 studied individual plants of *S. chinensis*. The former was significantly correlated to the latter ($r = 0.9923$ and $P < 0.001$). However, the Gini index for leaf area inequality measure significantly differed from that for leaf dry mass inequality measure based on the analysis result of the paired *t*-test ($P < 0.01$). The difference resulted from the allometric relationship between leaf dry mass and leaf area, and the numerical value of the scaling exponent of leaf dry mass vs. leaf area was significantly greater than unity. However, given the strong correlation between the two types of Gini indices, in practice, either can reflect the inequality extent of leaf size distribution per plant. It is promising to use the Gini index of leaf area inequality measure, because leaf area can be nondestructively measured using the product of leaf length and width multiplied by a proportionality coefficient. The present study provides a useful tool for measuring the inequality of leaf size distribution per plant, and it can quantify the influence of environments on the aboveground architectural structure of plants in future investigation.

Acknowledgments

We thank Bin Chen and Fusheng Wang for their valuable help in the preparation of this

work.

Author contributions

Meng Li & Peijian Shi: Formal analysis (equal); Methodology (equal); Writing – original draft (equal). Liuyue Zhang & Weihao Yao: Investigation (equal). Johan Gielis: Formal analysis (equal); Supervision (equal). Karl J. Niklas: Formal analysis (equal); Supervision (equal); Writing – review & editing (lead).

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Meng Lian http://orcid.org/ 0000-0002-9889-2507

Karl J. Niklas http://orcid.org/0000-0003-3491-1286

Liuyue Zhang http://orcid.org/0009-0005-3685-2541

Weihao Yao http://orcid.org/ 0000-0003-3872-0989

Johan Gielis https://orcid.org/0000-0002-4536-3839

Peijian Shi http://orcid.org/0000-0003-4696-0130

heeft opmaak toegepast

Data availability statement

All the raw data will be uploaded to Dryad, a public repository, when this manuscript is accepted. The raw data are temporarily tabulated in Table S1 at present.

References

Baird AS, Taylor SH, Pasquet-Kok JP, Vuong C, Zhang Y, Watcharamongkol T, Scoffoni S, Edwards EJ, Christin PA, Osborne CP. 2021. Developmental and biophysical determinants of grass leaf size worldwide. Nature 592: 242–247. doi: 10.1038/s41586-021-03370-0

Bruschi P, Grossoni P, Bussotti F. 2003. Within- and among-tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl. natural populations. Trees 17:164–172. doi: 10.1007/s00468-002-0218-y

Brière J-F, Pracros P, Le Roux A-Y, Pierre J-S. 1999. A novel rate model of temperature-dependent development for arthropods. Environ Entomol. 28: 22–29. doi: 10.1093/ee/28.1.22

de Casas RR, Vargas P, Pérez-Corona E, Manrique E, García-Verdugo C, Balaguer L. 2011. Sun and shade leaves of *Olea europaea* respond differently to plant size, light availability and genetic variation. Funct. Ecol. 25(4): 802−812. doi: 10.1111/j.1365-2435.2011.01851.x

Chen J, Chen J, Miao Y, Song M, Fan Y. 2016. Unbalanced development of inter-provincial high-grade highway in China: Decomposing the Gini coefficient. Transport Res D: Transport Environ. 48: 499–510. doi:10.1016/j.trd.2015.06.008

Chen BJW, During HJ, Vermeulen PJ, Anten NPR. 2014. The presence of a below-ground neighbour alters within-plant seed size distribution in *Phaseolus vulgaris*. Ann Bot. 114(5): 937–943. doi:10.1093/aob/mcu162

Chotikapanich D, Griffiths WE. 2002. Estimating Lorenz curves using a Dirichlet distribution. J Bus Econ Stata. 20: 290–295. doi: 10.1198/073500102317352029

Efron B, Tibshirani RJ. 1993. An introduction to the bootstrap. New York, NY: Chapman and Hall/CRC. doi: 10.1007/978-1-4899-4541-9

Gastwirth JL. 1971. A general definition of the Lorenz curve. Econometrica 39(6): 1037. doi:10.2307/1909675

Hara T. 1986. Effects of density and extinction coefficient on size variability in plant populations. Ann Bot. 57(6): 885–892. doi:10.1093/oxfordjournals.aob.a0871

Huang W, Reddy GVP, Li Y, Larsen, JB, Shi P. 2020. Increase in absolute leaf water content tends to keep pace with that of leaf dry mass—Evidence from bamboo plants. Symmetry 12: 1345. doi: 10.3390/sym12081345

Huey RB, Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Amer Zool. 19: 357–366.

Jin J, Quinn BK, Shi P. 2022. The modified Brière equation and its applications. Plants

11: 1769. doi: 10.3390/plants11131769

Küppers M. 1989. Ecological significance of above-ground architectural patterns in woody plants: a question of cost-benefit relationships. Trends Ecol Evol. 4: 375−379.

Lobry JR, Rosso L, Flandrois JP. 1991. A Fortran subroutine for the determination of parameter confidence limits in non-linear models. Binary 3: 86–93.

Lorenz MO. 1905. Methods of measuring the concentration of wealth. Am Statist Assoc. 70: 209−219.

Metsaranta JM, Lieffers VJ. 2008. Inequality of size and size Increment in *Pinus banksiana* in relation to stand dynamics and annual growth rate. Ann Bot. 101(4): 561–571. doi:10.1093/aob/mcm320

Milla R, Reich PB. 2007. The scaling of leaf area and mass: the cost of light interception increases with leaf size. Proc Roy Soc Biol Sci. 274(1622): 2109−2114. doi:10.1098/rspb.2007.0417.

Niklas KJ. 1994. Plant allometry: the scaling of form and process. Chicago: University of Chicago Press.

Niklas KJ, Cobb ED, Niinemets Ü, Reich PB, Sellin A, Shipley B, Wright IJ. 2007. “Diminishing returns” in the scaling of functional leaf traits across and within species groups. Proc Natl Acad Sci USA. 104: 8891–8896. doi: 10.1073/pnas.0701135104

Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytol. 182: 565–588. doi: 10.1111/j.1469-8137.2009.02830.x

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge, UK: Cambridge University Press, pp. 100−104.

R Core Team. 2022. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; [accessed 2022 June 1]. https://www.R-project.org/.

Ratkowsky DA, Lowry RK, McMeekin TA, Stokes AN, Chandler RE. 1983. Model for bacterial culture growth rate throughout the entire biokinetic temperature range. J

Bacteriol. 154: 1222–1226. doi: 10.1128/jb.149.1.1-5.1982

Rosso L, Lobry JR, Flandrois JP. 1993. An unexpected correlation between cardinal temperatures of microbial growth highlighted by a new model. J Theor Biol. 162: 447–463. doi: 10.1006/jtbi.1993.1099

Sandhu HS, Shi P, Kuang X, Xue F, Ge F. 2011. Applications of the bootstrap to insect physiology. Fla Entomol. 94: 1036–1041. doi: 10.1653/024.094.0442

Schrader J, Pillar G, Kreft H. 2017. Leaf-IT: an Android application for measuring leaf area. Ecol Evol 7: 9731–9738. doi: 10.1002/ece3.3485

Schrader J, Shi P, Royer DL, Peppe DJ, Gallagher RV, Li Y, Wang R, Wright IJ. 2021. Leaf size estimation based on leaf length, width and shape. Ann Bot. 128: 395–406. doi: 10.1093/aob/mcab078

Shi P, Fan M, Ratkowsky DA, Huang J, Wu H, Chen L, Fang S, Zhang C. 2017. Comparison of two ontogenetic growth equations for animals and plants. Ecol Model. 349: 1–10. doi: 10.1016/j.ecolmodel.2017.01.012

Shi P, Ge F, Sun Y, Chen C. 2011. A simple model for describing the effect of temperature on insect developmental rate. J Asia-Pac Entomol. 14: 15–20. doi: 10.1016/j.aspen.2010.11.008

Shi P, Gielis J, Quinn BK, Niklas KJ, Ratkowsky DA, Schrader J, Ruan H, Wang L, Niinemets Ü. 2022a. 'biogeom': An R package for simulating and fitting natural shapes. Ann N Y Acad Sci. 1516: 123–134. doi: 10.1111/nyas.14862

Shi P, Liu M, Ratkowsky DA, Gielis J, Su J, Yu X, Wang P, Zhang L, Lin Z, Schrader J. 2019. Leaf area–length allometry and its implications in leaf shape evolution. Trees Struct Funct 33: 1073–1085. doi: 10.1007/s00468-019-01843-4

Shi P, Ratkowsky DA, Li Y, Zhang L, Lin S, Gielis J. 2018. A general leaf area geometric formula exists for plants—Evidence from the simplified Gielis equation. Forests, 9: 714. doi: 10.3390/f9110714

Shi P, Ridland P, Ratkowsky D, Li Y. 2022b. IPEC: root mean square curvature calculation. R package version 1.0.3; [accessed 2022 June 1]. https://CRAN.R-project.org/package=IPEC.

Shi P, Xu Q, Sandhu HS, Gielis J, Ding Y, Li H, Dong X. 2015. 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. doi: 10.1002/ece3.1728

Sumida A, Terazawa I, Togashi A, Komiyama A. 2002. Spatial arrangement of branches in relation to slope and neighbourhood competition. Ann Bot. 89: 301–310. doi: 10.1093/aob/mcf042

Tanikawa T, Ohba H, Ogasawara K, Okuda Y, Ando Y. 2012. Geographical distribution of radiotherapy resources in Japan: Investigating the inequitable distribution of human resources by using the Gini coefficient. J Radiat Res. 53(3): 489–491. doi: 10.1269/jrr.11103.

Taylor KM, Aarssen LW. 1989. Neighbor effects in mast year seedlings of *Acer saccharum*. Am J Bot. 76(4): 546–554. doi:10.1002/j.1537-2197.1989.tb11346.x

Wang L, Shi P, Chen C, Xue F. 2013. Effect of Temperature on the Development of *Laodelphax striatellus* (Homoptera: Delphacidae). J Econ Entomol. 106(1): 107–114. doi:10.1603/ec12364

Wang P, Ratkowsky DA, Xiao X, Yu X, Su J, Zhang L, Shi P. 2018. Taylor's power law for leaf bilateral symmetry. Forests. 9: 500. doi: 10.3390/f9080500

Wang XJ, Zhang JY, Shahid S, EIMahdi A, He RM, Wang XG, Ali M. 2012. Gini coefficient to assess equity in domestic water supply in the Yellow River. Mitig Adapt Strateg Glob Change. 17: 65–75. doi: 10.1007/s11027-011-9309-7

Yin X, Kropff MJ, McLaren G, Visperas RM. 1995. A nonlinear model for crop development as a function of temperature. Agric Forest Meteorol. 77: 1–16. doi: 10.1016/0168-1923(95)02236-Q

Figure Legends

Figure 1. The Lorenz curve (a) and its rotated version (b) for household income. In panel (b), the rotated curve (i.e., the red curve) actually follows a performance equation. The Gini index is equal to the ratio of the area of shaded region to 1/2, i.e., half of the area of the unit square.

Figure 2. Illustration of the aboveground part of *Shibataea chinensis* Nakai.

Figure 3. The Lorenz curve (a) and its rotated version (b) for leaf area for a *S. chinensis* plant. AIC_1 represents the Akaike information criterion of the original performance equation (PE), i.e., equation (1); and AIC_2 represents Akaike information criterion of the generalized performance equation (GPE), i.e., equation (2). The data points are observations, and the curves are predicted values.

Figure 4. Comparison of the observed and predicted data of the accumulative proportion of leaf area vs. that of number of leaves per plants for each of the 12 individual plants (a-l). AIC_1 represents the Akaike information criterion of the original performance equation, i.e., equation (1); and AIC_2 represents Akaike information criterion of the generalized performance equation, i.e., equation (2). The data points are observations, and the curves are predicted values. The estimated values of model parameters, the coefficient of determination (i.e., r^2), and sample size (n, i.e., the number of leaves per plant) were also showed in each panel.

Figure 5. Comparison of the observed and predicted data of the accumulative proportion of leaf dry mass vs. that of number of leaves per plants for each of the 12 individual plants (a-l). AIC_1 represents the Akaike information criterion of the original performance equation, i.e., equation (1); and AIC_2 represents Akaike information criterion of the generalized performance equation, i.e., equation (2). The data points are observations, and the curves are predicted values. The estimated values of model parameters, the coefficient of determination (i.e., r^2), and sample size (n, i.e., the number of leaves per plant) were also showed in each panel.

Figure 6. Correlation between two types of Gini indices for leaf size.

Figure 7. The linear fits to leaf dry mass vs. leaf area for each of the 12 individuals of *S. chinensis*. In each panel, the open circles represent the observations, and the straight line represents the reduced major axis regression line; x represents the logarithm of leaf area (cm^2); y represents the logarithm of leaf dry mass in grams; CI represents the 95% confidence intervals of the slope of leaf dry mass vs. area; r^2 is the coefficient of determination; and n represents the number of leaves sampled. The colors of the open circles represent different individuals.

Figure 8. Comparison between the observed and predicted leaf area (A) by the Montgomery equation for 12 individuals of *S. chinensis*, represented as log-log plots of A vs. the product of leaf length (L) and width (W). Here, 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 individual), $\hat{k}$ represents the estimated Montgomery parameter, and 95% CI represents the 95% confidence interval of each Montgomery parameter estimate. Panels (a–l) represent the fitted results for different individuals. 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. The colors of the open circles represent different individuals.

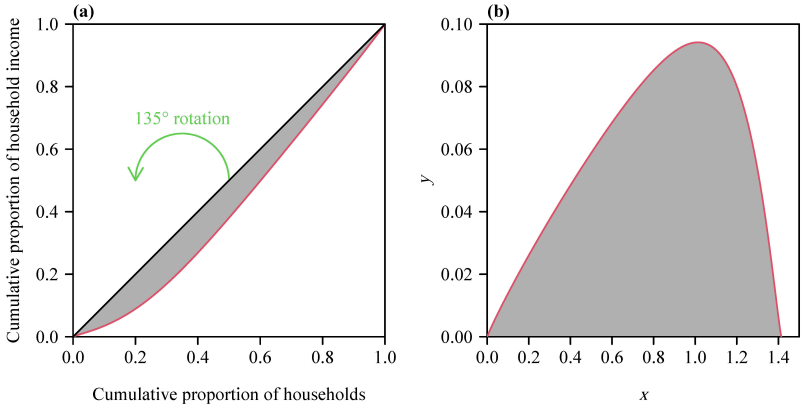
(a)
Cumulative proportion of household income
1.0
0.8
0.6
0.4
0.2
0.0
135° rotation
0.0
0.2
0.4
0.6
0.8
1.0
Cumulative proportion of households
(b)
0.10
0.08
0.06
0.04
0.02
0.00
y
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
x

Figure 1

Figure 2

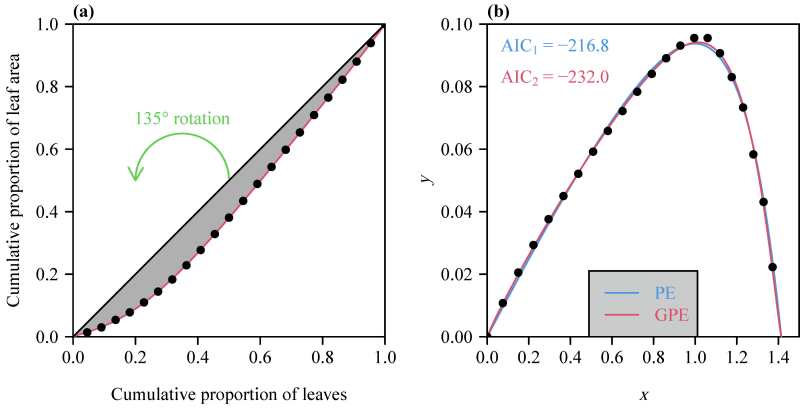
(a)
1.0
0.8
0.6
0.4
0.2
0.0
Cumulative proportion of leaf area
135° rotation
0.0
0.2
0.4
0.6
0.8
1.0
Cumulative proportion of leaves
(b)
0.10
0.08
0.06
0.04
0.02
0.00
y
AIC1 = −216.8
AIC2 = −232.0
PE
GPE
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
x

Figure 3

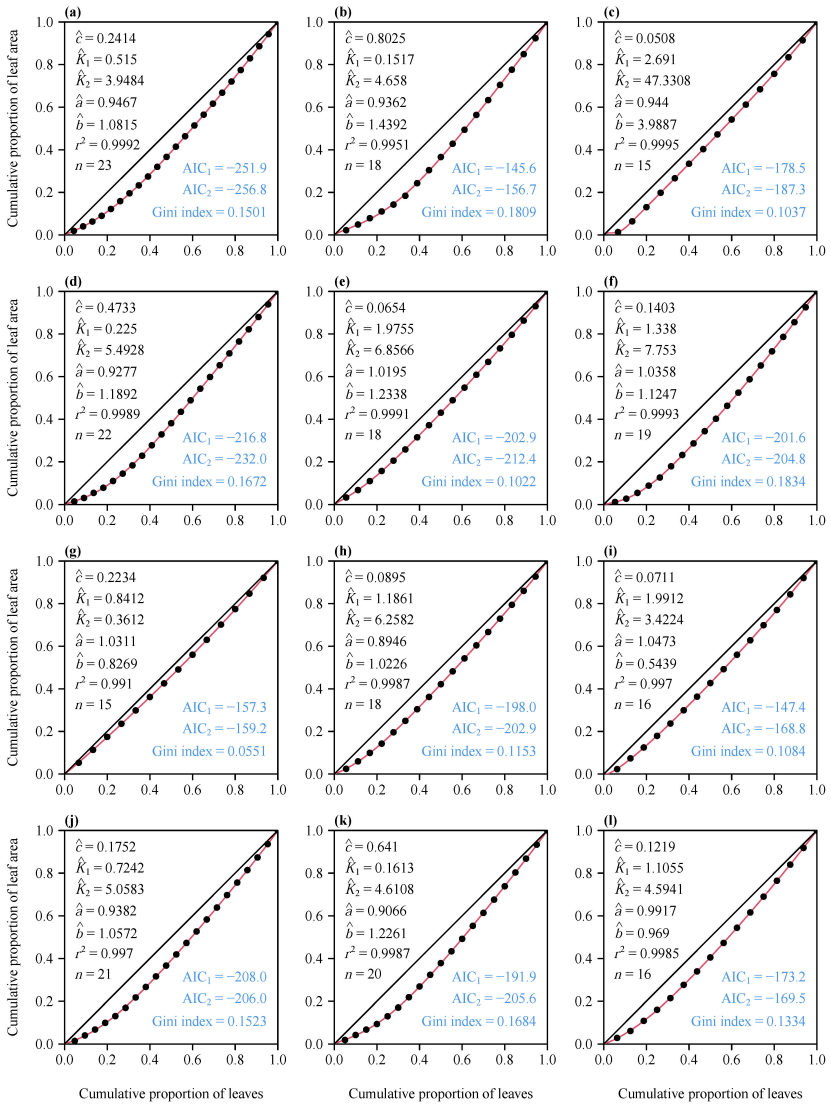
(a)
$\hat{c}$ = 0.2414
$\hat{K}_1$ = 0.515
$\hat{K}_2$ = 3.9484
$\hat{a}$ = 0.9467
$\hat{b}$ = 1.0815
r^2 = 0.9992
n = 23
AIC$_1$ = −251.9
AIC$_2$ = −256.8
Gini index = 0.1501
(b)
$\hat{c}$ = 0.8025
$\hat{K}_1$ = 0.1517
$\hat{K}_2$ = 4.658
$\hat{a}$ = 0.9362
$\hat{b}$ = 1.4392
r^2 = 0.9951
n = 18
AIC$_1$ = −145.6
AIC$_2$ = −156.7
Gini index = 0.1809
(c)
$\hat{c}$ = 0.0508
$\hat{K}_1$ = 2.691
$\hat{K}_2$ = 47.3308
$\hat{a}$ = 0.944
$\hat{b}$ = 3.9887
r^2 = 0.9995
n = 15
AIC$_1$ = −178.5
AIC$_2$ = −187.3
Gini index = 0.1037
(d)
$\hat{c}$ = 0.4733
$\hat{K}_1$ = 0.225
$\hat{K}_2$ = 5.4928
$\hat{a}$ = 0.9277
$\hat{b}$ = 1.1892
r^2 = 0.9989
n = 22
AIC$_1$ = −216.8
AIC$_2$ = −232.0
Gini index = 0.1672
(e)
$\hat{c}$ = 0.0654
$\hat{K}_1$ = 1.9755
$\hat{K}_2$ = 6.8566
$\hat{a}$ = 1.0195
$\hat{b}$ = 1.2338
r^2 = 0.9991
n = 18
AIC$_1$ = −202.9
AIC$_2$ = −212.4
Gini index = 0.1022
(f)
$\hat{c}$ = 0.1403
$\hat{K}_1$ = 1.338
$\hat{K}_2$ = 7.753
$\hat{a}$ = 1.0358
$\hat{b}$ = 1.1247
r^2 = 0.9993
n = 19
AIC$_1$ = −201.6
AIC$_2$ = −204.8
Gini index = 0.1834
(g)
$\hat{c}$ = 0.2234
$\hat{K}_1$ = 0.8412
$\hat{K}_2$ = 0.3612
$\hat{a}$ = 1.0311
$\hat{b}$ = 0.8269
r^2 = 0.991
n = 15
AIC$_1$ = −157.3
AIC$_2$ = −159.2
Gini index = 0.0551
(h)
$\hat{c}$ = 0.0895
$\hat{K}_1$ = 1.1861
$\hat{K}_2$ = 6.2582
$\hat{a}$ = 0.8946
$\hat{b}$ = 1.0226
r^2 = 0.9987
n = 18
AIC$_1$ = −198.0
AIC$_2$ = −202.9
Gini index = 0.1153
(i)
$\hat{c}$ = 0.0711
$\hat{K}_1$ = 1.9912
$\hat{K}_2$ = 3.4224
$\hat{a}$ = 1.0473
$\hat{b}$ = 0.5439
r^2 = 0.997
n = 16
AIC$_1$ = −147.4
AIC$_2$ = −168.8
Gini index = 0.1084
(j)
$\hat{c}$ = 0.1752
$\hat{K}_1$ = 0.7242
$\hat{K}_2$ = 5.0583
$\hat{a}$ = 0.9382
$\hat{b}$ = 1.0572
r^2 = 0.997
n = 21
AIC$_1$ = −208.0
AIC$_2$ = −206.0
Gini index = 0.1523
(k)
$\hat{c}$ = 0.641
$\hat{K}_1$ = 0.1613
$\hat{K}_2$ = 4.6108
$\hat{a}$ = 0.9066
$\hat{b}$ = 1.2261
r^2 = 0.9987
n = 20
AIC$_1$ = −191.9
AIC$_2$ = −205.6
Gini index = 0.1684
(l)
$\hat{c}$ = 0.1219
$\hat{K}_1$ = 1.1055
$\hat{K}_2$ = 4.5941
$\hat{a}$ = 0.9917
$\hat{b}$ = 0.969
r^2 = 0.9985
n = 16
AIC$_1$ = −173.2
AIC$_2$ = −169.5
Gini index = 0.1334
Cumulative proportion of leaf area
Cumulative proportion of leaves
0.0
0.2
0.4
0.6
0.8
1.0

Figure 4

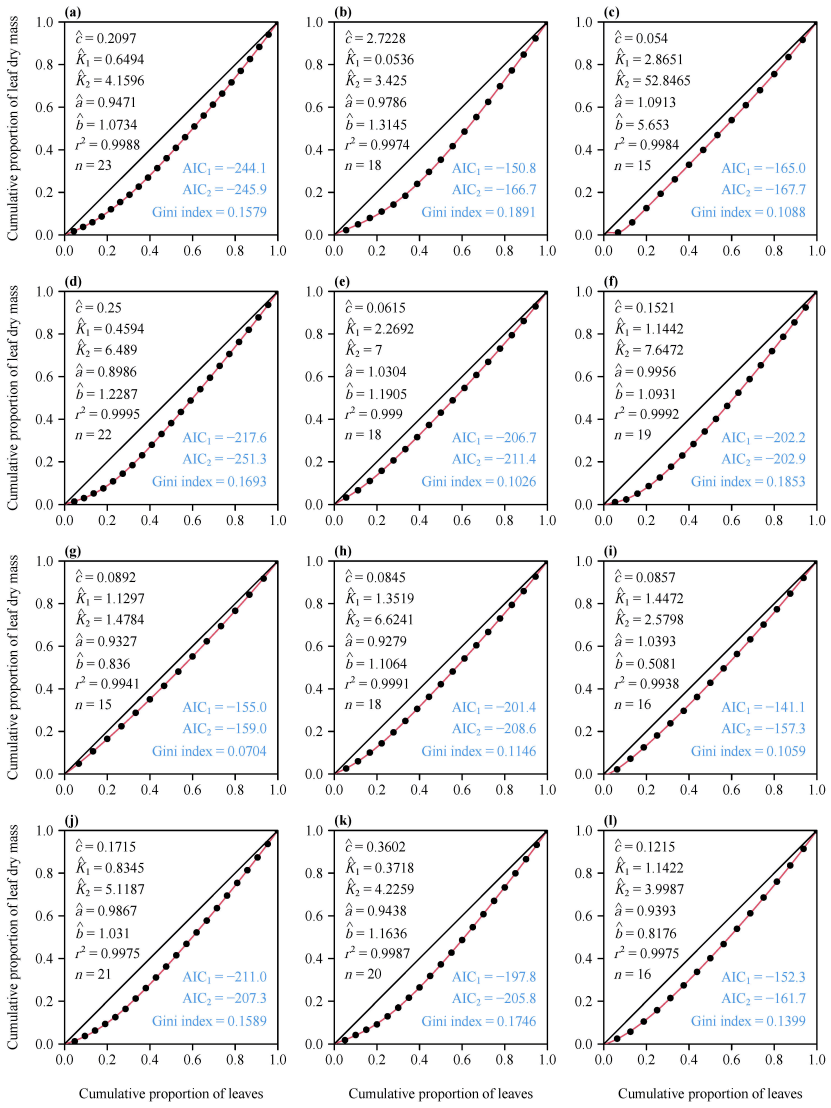
(a)
$\hat{c}$ = 0.2097
$\hat{K}_1$ = 0.6494
$\hat{K}_2$ = 4.1596
$\hat{a}$ = 0.9471
$\hat{b}$ = 1.0734
r^2 = 0.9988
n = 23
AIC$_1$ = −244.1
AIC$_2$ = −245.9
Gini index = 0.1579
(b)
$\hat{c}$ = 2.7228
$\hat{K}_1$ = 0.0536
$\hat{K}_2$ = 3.425
$\hat{a}$ = 0.9786
$\hat{b}$ = 1.3145
r^2 = 0.9974
n = 18
AIC$_1$ = −150.8
AIC$_2$ = −166.7
Gini index = 0.1891
(c)
$\hat{c}$ = 0.054
$\hat{K}_1$ = 2.8651
$\hat{K}_2$ = 52.8465
$\hat{a}$ = 1.0913
$\hat{b}$ = 5.653
r^2 = 0.9984
n = 15
AIC$_1$ = −165.0
AIC$_2$ = −167.7
Gini index = 0.1088
(d)
$\hat{c}$ = 0.25
$\hat{K}_1$ = 0.4594
$\hat{K}_2$ = 6.489
$\hat{a}$ = 0.8986
$\hat{b}$ = 1.2287
r^2 = 0.9995
n = 22
AIC$_1$ = −217.6
AIC$_2$ = −251.3
Gini index = 0.1693
(e)
$\hat{c}$ = 0.0615
$\hat{K}_1$ = 2.2692
$\hat{K}_2$ = 7
$\hat{a}$ = 1.0304
$\hat{b}$ = 1.1905
r^2 = 0.999
n = 18
AIC$_1$ = −206.7
AIC$_2$ = −211.4
Gini index = 0.1026
(f)
$\hat{c}$ = 0.1521
$\hat{K}_1$ = 1.1442
$\hat{K}_2$ = 7.6472
$\hat{a}$ = 0.9956
$\hat{b}$ = 1.0931
r^2 = 0.9992
n = 19
AIC$_1$ = −202.2
AIC$_2$ = −202.9
Gini index = 0.1853
(g)
$\hat{c}$ = 0.0892
$\hat{K}_1$ = 1.1297
$\hat{K}_2$ = 1.4784
$\hat{a}$ = 0.9327
$\hat{b}$ = 0.836
r^2 = 0.9941
n = 15
AIC$_1$ = −155.0
AIC$_2$ = −159.0
Gini index = 0.0704
(h)
$\hat{c}$ = 0.0845
$\hat{K}_1$ = 1.3519
$\hat{K}_2$ = 6.6241
$\hat{a}$ = 0.9279
$\hat{b}$ = 1.1064
r^2 = 0.9991
n = 18
AIC$_1$ = −201.4
AIC$_2$ = −208.6
Gini index = 0.1146
(i)
$\hat{c}$ = 0.0857
$\hat{K}_1$ = 1.4472
$\hat{K}_2$ = 2.5798
$\hat{a}$ = 1.0393
$\hat{b}$ = 0.5081
r^2 = 0.9938
n = 16
AIC$_1$ = −141.1
AIC$_2$ = −157.3
Gini index = 0.1059
(j)
$\hat{c}$ = 0.1715
$\hat{K}_1$ = 0.8345
$\hat{K}_2$ = 5.1187
$\hat{a}$ = 0.9867
$\hat{b}$ = 1.031
r^2 = 0.9975
n = 21
AIC$_1$ = −211.0
AIC$_2$ = −207.3
Gini index = 0.1589
(k)
$\hat{c}$ = 0.3602
$\hat{K}_1$ = 0.3718
$\hat{K}_2$ = 4.2259
$\hat{a}$ = 0.9438
$\hat{b}$ = 1.1636
r^2 = 0.9987
n = 20
AIC$_1$ = −197.8
AIC$_2$ = −205.8
Gini index = 0.1746
(l)
$\hat{c}$ = 0.1215
$\hat{K}_1$ = 1.1422
$\hat{K}_2$ = 3.9987
$\hat{a}$ = 0.9393
$\hat{b}$ = 0.8176
r^2 = 0.9975
n = 16
AIC$_1$ = −152.3
AIC$_2$ = −161.7
Gini index = 0.1399
Cumulative proportion of leaf dry mass
Cumulative proportion of leaves
0.0
0.2
0.4
0.6
0.8
1.0

Figure 5

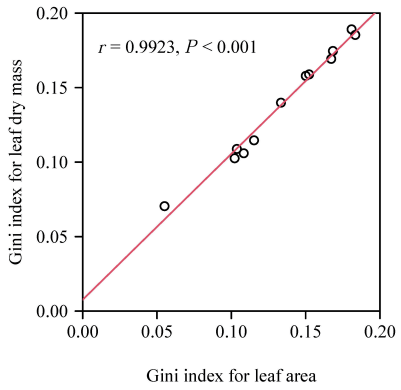
r = 0.9923, P < 0.001
Gini index for leaf dry mass
Gini index for leaf area
0.00
0.05
0.10
0.15
0.20

Figure 6

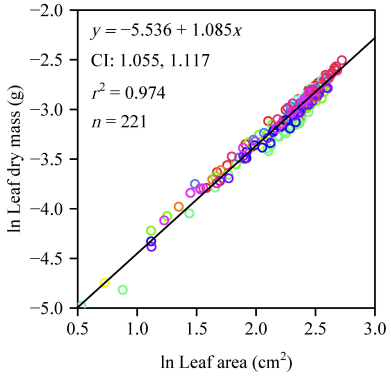
y = −5.536 + 1.085x
CI: 1.055, 1.117
r2 = 0.974
n = 221
ln Leaf dry mass (g)
ln Leaf area (cm2)
−2.0
−2.5
−3.0
−3.5
−4.0
−4.5
−5.0
0.5
1.0
1.5
2.0
2.5
3.0

Figure 7

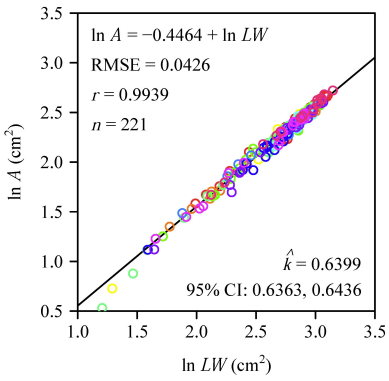
ln A = −0.4464 + ln LW
RMSE = 0.0426
r = 0.9939
n = 221
k̂ = 0.6399
95% CI: 0.6363, 0.6436
ln A (cm²)
ln LW (cm²)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5

Figure 8