Scaling the leaf length-times-width equation to predict total leaf area of shoots

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• Background and Aims An individual plant consists of different-sized shoots, each of which consists of different-sized leaves. To predict plant-level physiological responses from the responses of individual leaves, modelling this within-shoot leaf size variation is necessary. Within-plant leaf trait variation has been well investigated in canopy photosynthesis models but less so in plant allometry. Therefore, integration of these two different approaches is needed.

• Methods We focused on an established leaf-level relationship that the area of an individual leaf lamina is proportional to the product of its length and width. The geometric interpretation of this equation is that different-sized leaf lamina from a single species share the same basic form. Based on this shared basic form, we synthesized a new length-times-width equation predicting total shoot leaf area from the collective dimensions of leaves that comprise a shoot. Furthermore, we showed that several previously established empirical relationships, including the allometric relationships between total shoot leaf area, maximum individual leaf length within the shoot and total leaf number of the shoot, can be unified under the same geometric argument. We tested the model predictions using five species, all of which have simple leaves, selected from diverse taxa (Magnoliids, monocots and eudicots) and from different growth forms (trees, erect herbs and rosette herbs).

• Key Results For all five species, the length-times-width equation explained within-species variation of total leaf area of a shoot with high accuracy ($R^2 > 0.994$). These strong relationships existed despite leaf dimensions scaling very differently between species. We also found good support for all derived predictions from the model ($R^2 > 0.85$).

• Conclusions Our model can be incorporated to improve previous models of allometry that do not consider within-shoot size variation of individual leaves, providing a cross-scale linkage between individual leaf-size variation and shoot-size variation.

Key words: Allometry, scaling, leaf size, shoot size, intraspecific, Corner’s rule, self-affine, Cardiocrinum cordatum, Fallopia sachalinensis, Magnolia kobus, Prunus sargentii, Ulmus davidiana var. japonica.

INTRODUCTION

Plants are modular organisms, and they can be considered as a population of leaves and stems (Harper and Bell, 1979). Within each plant, organs (e.g. leaf or stem) usually differ in size, physiology and microenvironments (Field, 1983; DeJong et al., 1989; Koyama and Kikuzawa, 2010; Niinemets, 2016; Kusi and Karsai, 2020; Maslova et al., 2021). Therefore, photosynthesis of individual plants or ecosystems has been modelled as the sum of those of individual leaves (Bazzaz and Harper, 1977; Field, 1983; Ackerly and Bazzaz, 1995; Koyama and Kikuzawa, 2009). This cross-scale relationship between organ-level and plant- or ecosystem-level physiology has long been recognized as one of the central issues in canopy photosynthesis models (Field, 1991; Hikosaka et al., 2016; Niinemets, 2016).

However, despite its importance, within-canopy or within-plant variation of organs has rarely been incorporated in the field of plant allometry. Allometry (i.e. power functions) has been a successful tool for analysing relationships between the properties of different-sized individual plants or organs (Niklas, 1994; Enquist et al., 2009; Mori et al., 2010; Savage et al., 2010; Bentley et al., 2013; Okie, 2013; Banavar et al., 2014; Huang et al., 2019; Lin et al., 2020; Olson et al., 2020; Kurosawa et al., 2021; Wang et al., 2021). However, most plant-level allometric models are based on the simplifying assumption that each individual plant has terminal organs (twigs or leaves) of the same size (Enquist et al., 2009; West et al., 2009; Savage et al., 2010; Banavar et al., 2014). These approaches contrast with organ-level studies on the within-plant size variation of twigs and leaves (Dombroskie and Aarssen, 2012; Koyama et al., 2012, 2017; Kusi and Karsai, 2020; Maslova et al., 2021). The integration of these two approaches, plant allometry and canopy photosynthesis models, has not been achieved yet, although both approaches independently predict plant- or ecosystem-level metabolism (Koyama et al., 2017).

Here, a shoot is defined as a terminal single current-year stem with all its appendages (leaves, buds, flowers, fruits, etc.). A shoot is equivalent to an individual ramet (i.e. whole aboveground part of a plant) in single-stem herbaceous species. For trees, a shoot is a fundamental unit of growth (Sterck et al., 2021).
2005; Sterck and Schievling, 2007; Lecigne et al., 2021) and reproduction (Chen et al., 2009; Scott and Aarssen, 2013; Miranda et al., 2019; Fajardo et al., 2020). Given its importance, allometric relationships of shoot size and total shoot leaf area have been important topics in plant ecophysiology (Corner, 1949; White, 1983; Ackerly and Donoghue, 1998; Brouat et al., 1998; Westoby and Wright, 2003; Kleiman and Aarssen, 2007; Olson et al., 2009, 2018; Sun et al., 2010, 2020, Yan et al., 2013; Trueba et al., 2016; Fan et al., 2017; Smith et al., 2017; Zhu et al., 2019; Fajardo et al., 2020). However, most previous studies on leaf vs. shoot size allometry have focused on the relationship among shoot size, total shoot leaf area, total leaf number and/or mean individual leaf size on the shoot. These studies are not mutually exclusive of, but do not yet have a theoretical connection with, the fact mentioned above that a shoot has a population of leaves with a size distribution (see Bazzaz and Harper, 1977). Because the total leaf area of a shoot (or a plant) is the sum of the areas of individual leaves, the leaf size distribution within a shoot is one of the main determinants of whole-plant or total shoot leaf area (Seleznyova and Greer, 2001; Bultynck et al., 2004). Yet, with only a few exceptions (e.g. Koyama et al., 2012; Smith et al., 2017), this fact was not considered in most previous studies on leaf size – shoot size allometry (e.g. Sun et al., 2006, 2010, 2017, 2019a, b, 2020; Kleiman and Aarssen, 2007; Ogawa, 2008; Yang et al., 2008, 2009, 2010; Milla, 2009; Xiang et al., 2009a, 2010; Whitman and Aarssen, 2010; Dombrowski and Aarssen, 2012; Scott and Aarssen, 2012, 2013; Yan et al., 2013; Dombrowski et al., 2016; Trueba et al., 2016; Olson et al., 2018; Miranda et al., 2019; Zhu et al., 2019; Fajardo et al., 2020).

Therefore, the objective of this study was to clarify the relationship between size variations at two different levels: the within-species size variation of shoots and the within-shoot size variation of leaves. We propose a simple geometric model that incorporates these two size variations. The model is a mathematical quantification and generalization of the results of Koyama et al. (2012), which showed that differently sized plants of the herbaceous species Cardiocrinum cordatum share the same basic structure. However, their study did not provide a mathematical model that could derive these relationships. Furthermore, the present model is more general than the findings of Koyama et al. (2012), in that it can be applied to various plant forms (trees, rosettes and erect herbs). In the present model, maximum leaf size within a shoot plays a pivotal role. In relation to this, Sun et al. (2019a, 2020) recently proposed a model that unified previous studies on the leaf size-number trade-off (Kleiman and Aarssen, 2007), shoot photosynthesis and growth (Niklas and Enquist, 2001, 2002), and stem cross-sectional area [i.e. pipe model (Shinozaki et al., 1964; Brouat et al., 1998)]. Sun et al. (2019a, 2020) also found that maximum leaf size within a shoot is a major determinant of the leaf number per stem mass across different species. Moreover, Lopes and Pinto (2005), and Heerema, Spann, and their colleagues (Heerema et al., 2008; Spann and Heerema, 2010) proposed empirical relationships that use maximum leaf size to predict total shoot leaf area. Nonetheless, all of these previous findings, specifically on the usefulness of maximum leaf size, are phenomenological because they do not provide any quantitative model to explain why maximum leaf size is a predictor of the total leaf area of a shoot. Here, we used an entirely novel approach, which uses maximum leaf size to model within-shoot and between-shoot leaf size variations.

MODEL

Individual leaf area (\(A_{\text{leaf}}\)) is defined as the area of one side of each lamina (i.e. leaf blade) (John et al., 2017). A shoot may have one or multiple leaves, each of which may differ in size. Therefore, the total leaf area of a shoot (\(A_{\text{shoot}}\)) is defined as the sum of \(A_{\text{leaf}}\) of all the leaves on that shoot:

\[
A_{\text{shoot}} = \sum_{\text{leaf}} A_{\text{leaf}}
\]  

(1)

The symbol ‘\(\equiv\)’ indicates ‘defined as’. As our aim was to find simple formulas that predict \(A_{\text{shoot}}\), taking into consideration the within-shoot size variation of \(A_{\text{leaf}}\), the present model is based on several simplifications. (1) We focused only on the leaf laminae that determine \(A_{\text{shoot}}\). We thus ignored any other organs (e.g. stem, petioles, buds and reproductive organs). (2) Our model only deals with simple leaves with flat-shaped laminae: the current model cannot be applied to leaves of different forms (e.g. compound leaves that consist of multiple leaflets, succulent leaves or conifer needles). The limitations associated with these simplifications will be addressed in the Discussion.

We use the two words ‘similar’ and ‘affine’ (Fig. 1), which have been used as compound words ‘self-similar’ and ‘self-affine’ in fractal geometry (Falconer, 2003; Okie, 2013; Shi et al., 2021b). In Fig. 1, in each panel (A and B), the two green triangles represent two different-sized individual leaf laminae. Two shapes are similar if they can be made identical by multiplying each dimension by a single constant (i.e. similar transformation). Two shapes are affine if they can be made identical by multiplying each dimension by a different constant (i.e. affine transformation).

First, we focused on individual leaves. Within a species, the area of an individual leaf (\(A_{\text{leaf}}\)) is proportional to the lamina length (\(L_{\text{leaf}}\)) times lamina width (\(W_{\text{leaf}}\)) (Cain and Castro, 1959; Teobaldelli et al., 2019a, b; Yu et al., 2020; Huang et al., 2021; Li et al., 2021; Schrader et al., 2021; Shi et al., 2021a) (Fig. 2A):

\[
A_{\text{leaf}} \propto L_{\text{leaf}} \times W_{\text{leaf}}
\]  

(2)

The symbol ‘\(\propto\)’ indicates ‘proportional to’. Equation (2) is known as the Montgomery equation (Yu et al., 2020; Shi et al., 2021a). It indicates that leaves from the same species are affine to each other.

Next, we extend eqn (2) to the level of shoots to predict \(A_{\text{shoot}}\). We hypothetically detach all the leaf laminae from the stem,
The length-times-width equation for shoot leaf area is given by eqn (4):

$$A_{\text{shoot}} \propto L_{f} \times W_{f}$$

We refer to this set of leaf laminae as the ‘foliage’ of each shoot. The subscripts ‘f’ in eqn (3) stand for ‘foliage’. We exclude petioles because they contribute to the 3D arrangement with relatively little contribution to $A_{\text{shoot}}$. The utility of rearranging the leaves is that both foliage length ($L_{f}$) and foliage width ($W_{f}$) can be defined independently from the 3D arrangement of the leaves. Our main hypothesis is that, within a single species, different-sized sets of foliage are affine, and therefore follows the allometric relationship:

$$L_{f} \propto W_{f}^{\beta} \quad (\beta > 1)$$

The exponent $\beta$ is expected to be $>1$, for the following reason. If foliage always consists of a single leaf, irrespective of its size, by definition $L_{f}$ and $W_{f}$ are equivalent to $W_{\text{leaf}}$ and $L_{\text{leaf}}$, respectively. In this case, $L_{f}$ and $W_{f}$ should be approximately proportional to each other (i.e. $\beta = 1$). However, in reality, a shoot usually has multiple leaves. Because $L_{f}$ is defined as the sum of the widths of all leaves, larger foliage with more leaves should have a disproportionately larger length relative to its width than small foliage ($\beta > 1$). In general, the value of $\beta$ may vary among species, depending on the species’ intrinsic maximum leaf size and leafing intensity. In the Results, we show that eqn (5) is valid. Before demonstrating this, we proceed by assuming that eqn (5) is valid to derive other predictions. By combining eqns (4) and (5), we obtained:

$$A_{\text{shoot}} \propto \left[ \max_{\text{shoot}} (L_{\text{leaf}}) \right]^{\beta+1}$$

(6)

As mentioned above, the lamina area of an individual leaf is predicted by the product of lamina length and width with high accuracy (i.e. high $R^{2}$ values). Additionally, it is known that individual leaf area can also be predicted by a quadratic function of lamina length or width alone [e.g. $A_{\text{leaf}} \propto (L_{\text{leaf}})^{2}$], albeit with less accuracy (Teobaldelli et al., 2019a, b). Similarly, eqn (6) predicts that $A_{\text{shoot}}$ can also be predicted by $W_{f}$ alone, with less but acceptable accuracy. Note that because $\beta > 1$, the exponent is expected to be $>2$. Suppose we further use an empirical relationship that individual lamina length is approximately proportional to lamina width [$L_{\text{leaf}} \propto W_{\text{leaf}}$ (Ogawa et al., 1995)], by using eqn (6), we predicted that the maximum leaf lamina width within a shoot can also be used as a predictor of $A_{\text{shoot}}$:

$$A_{\text{shoot}} \propto \left[ \max_{\text{shoot}} (W_{\text{leaf}}) \right]^{\beta+1}$$

(7)

These predictions [eqns (6) and (7)] were also tested in this study. Previous studies have already recognized the usefulness of maximum leaf size as a predictor of $A_{\text{shoot}}$ (Lopes and Pinto, 2005; Heerema et al., 2008; Sun et al., 2019a; Teobaldelli et al., 2020). However, these studies used maximum leaf size only as empirical models. Therefore, none of them has provided a quantitative theory that explains why this relationship holds. In the following subsections, we show that these empirical relationships can also be derived as corollaries of the present model.

Sun et al.’s equation

Sun et al. (2019a, 2020) found that $A_{\text{shoot}}$ is proportional to the product of the maximum leaf area and total number of leaves on each shoot ($N$), because the maximum individual leaf area of a shoot corresponds to its potential leaf-producing capacity. This relationship can also be derived from our model (see Appendix for derivation):

$$A_{\text{shoot}} \propto N \cdot \max_{\text{shoot}} (A_{\text{leaf}})$$

(8)

We retest this prediction in this study.
Size–number allometry

We also derived the allometric relationship between $A_{\text{shoot}}$ and the total number of leaves on each shoot ($N$) reported by Koyama et al. (2012) (see Appendix for derivation):  
\[
A_{\text{shoot}} \propto N^\alpha,
\]
where \( \alpha \equiv \frac{\beta + 1}{\beta - 1} = 1 + \frac{2}{\beta - 1} > 1 (\because \beta > 1) \) (9)

Generally, the exponent $\alpha$ may vary depending on species as a function of $\beta$. The predicted allometric relationship between $A_{\text{shoot}}$ and $N$ with the exponent $\alpha > 1$ (given $\beta > 1$) agrees with the empirical result reported by Koyama et al. (2012). We retested this prediction in this study. In addition, eqn (9) can be rearranged to predict the scaling relationship between mean individual leaf area ($=A_{\text{shoot}}/N$) and $A_{\text{shoot}}$ with the exponent $0 < \lambda < 1$ (see Appendix for derivation):  
\[
\frac{A_{\text{shoot}}}{N} \propto (A_{\text{shoot}})^\lambda,
\]
where  
\[
\lambda \equiv 1 - \frac{1}{\alpha} = \frac{2}{\beta + 1}
\]
(10)

The prediction that $0 < \lambda < 1$ was empirically supported by Smith et al. (2017).

Heerema–Spann–Teobaldelli et al.'s equation

Heerema, Spann, and their colleagues (Heerema et al., 2008; Spann and Heerema, 2010) reported an empirical relationship that $A_{\text{shoot}}$ can be predicted by the maximum leaf length of a shoot (i.e. foliage width, $W_f$) and the total number of leaves on that shoot ($N$) using woody fruit crop species. Teobaldelli et al. (2020) modified this relationship into a general allometric form. These relationships can also be derived from our model (see Appendix for derivation):  
\[
A_{\text{shoot}} \propto W_f \cdot N^\gamma,
\]
where  
\[
\gamma \equiv \frac{\beta}{\beta - 1} = 1 + \frac{1}{\beta - 1} (\because \beta > 1)
\]
(11)

Equation (11) was proposed as an empirical model by Teobaldelli et al. (2020), which includes the formula proposed by Heerema, Spann and their colleagues as a specific case when $\gamma = 1$, which does not take into consideration the $\beta$-dependency of $\gamma$. Generally, $\gamma$ may vary among species as a function of $\beta$. Here, eqn (11) was tested by the following allometric relationship:  
\[
A_{\text{shoot}} \propto W_f
\]
(12)

We also directly tested eqn (12). Unlike eqns (4) and (5), eqn (12) does not use foliage length ($L_f$) as a variable, and therefore eqn (12) can be tested independently.

Lopes–Pinto’s equation

Lopes and Pinto (2005) found an empirical formula that predicts $A_{\text{shoot}}$ for a wine grape variety using the maximum and minimum leaf area within each shoot. They found that each shoot’s mean individual leaf area can be estimated as the mean of maximum and minimum leaf area within that shoot. This relationship can also be derived from our model (see Appendix for derivation):  
\[
A_{\text{shoot}} = k \cdot N \left[ \min_{\text{leaf}} \left( \frac{A_{\text{leaf}}}{2} \right) + \max_{\text{leaf}} \left( \frac{A_{\text{leaf}}}{2} \right) \right]
\]
(13)

The symbol $k$ is a proportionality constant. Lopes, Pinto and colleagues (Lopes and Pinto, 2005; Phinopoulos et al., 2015) found the same relationship as eqn (13) for two wine grape varieties as an empirical formula. They used an empirical value of $k = 1$ (i.e. in their cases, mean individual leaf area was simply the average value of the largest and the smallest leaves) as a specific value for the grape varieties. Generally, $k$ may vary depending on the species (depending on the arrangement of different-sized leaves along a shoot). This prediction was also tested in this study.

MATERIALS AND METHODS

Study species

The study species and the sample sizes are listed in Table 1. Each species is referred to by its genus name after its first mention. All species have simple leaves with reticulate or reticulate-like venation patterns. (1) Kobushi magnolia (Magnolia kobus, Magnoliaceae). Magnolia was selected because it is taxonomically separate from the other species (APG IV, 2016). (2) Cardiocrinum cordatum (including var. glehni) (Liliaceae) is a monocarpic perennial herb. This species belongs to the monocots (APG IV, 2016), but its leaves have reticulate venation patterns that are similar to those of eudicots (see photographs in Koyama et al., 2012). Small individual plants form rosettes on the ground without elongating their stems, whereas large plants become bolting rosettes, which elongate their vertical stems with flower buds on top (Ohara et al., 2006; Komamura et al., 2021). (3) Sargent’s cherry (Prunus sargentii, Rosaceae) and (4) Japanese elm (Ulmus davidiana var. japonica, Ulmaceae). Prunus and Ulmus were chosen as typical broadleaved deciduous trees in temperate forests. (5) Giant knotweed (Fallopia sachalinensis, Polygonaceae) is a high-stature erect herb (plant height often reaches 2–3 m) with large leaves along its vertical stem. Cardiocrinum and Fallopia were chosen because they have contrasting growth forms (rosette vs. erect) and are from different taxonomic groups (monocot vs. eudicot).

Field sampling

A shoot is defined herein as a single current-year stem with its appendages (leaves, buds, flowers, fruits, etc.). For the two single-stemmed herbaceous species (Cardiocrinum and Fallopia), a shoot is equivalent to an entire above-ground part of an individual ramet, and therefore $A_{\text{shoot}}$ is equivalent to whole-plant leaf area. Sample sizes and the sampling locations are given in Table 1. Sampling was conducted in summer (June–August) in 2016 and 2020. All sampling sites were located in Obihiro City or the adjacent Otofuke Town in Hokkaido Island.
in a cool-temperate region of Japan, and were within 10 km from the Obihiro Weather Station (42°52′N 143°10′E, altitude: 76 m a.s.l.). Mean annual temperature and precipitation at the weather station during 1998–2017 were 7.2 °C and 937 mm, respectively (Japan Meteorological Agency, 2020). Shoots with obvious damage (e.g. leaf loss due to herbivory etc.) were excluded. For the woody species, shoots that had sylleptic shoots (i.e. branching within the current year) were not sampled. Our sampling strategy was not random, but instead the shoots were sampled to cover a wide range sizes within each

### Table 1. Study species and sample sizes

| Taxonomy       | Magnoliid (Magnoliiales, Magnoliaceae) | Monocot (Liliales, Liliaceae) | Eudicot (Rosales, Rosaceae) | Eudicot (Rosales, Ulmaceae) | Eudicot (Caryophyllales, Polygonaceae) |
|----------------|----------------------------------------|--------------------------------|-----------------------------|-----------------------------|----------------------------------------|
| Growth form    | Tree (deciduous)                       | Herb (rosette or bolting)     | Tree (deciduous)             | Tree (deciduous)             | Erect herb                             |
| Location       | R, T                                   | F, H                          | U                           | U, F                        | U                                      |
| Number of shoots investigated | 37                                     | 36                            | 39                          | 43                          | 29                                     |
| Size ranges \(A_{shoot} (\text{cm}^2)\) | min 11.3                               | 11.6                          | 9.5                         | 1.2                         | 62.3                                   |
|                | max 1440.8                             | 5718.2                        | 1884.6                      | 652.3                       | 11 716.5                               |
| \(N\)          | min 2                                  | 1                             | 1                           | 1                           | 4                                      |
|                | max 11                                 | 22                            | 20                          | 15                          | 19                                     |

Location of sampling: F: The Forest of Obihiro; H: natural forest preservation of Hokkaido Obihiro Agricultural High School; R: Urikari River; T: Tokachi Ecology Park; U: Obihiro University of Agriculture and Veterinary Medicine. \(A_{\text{shoot}}\): total leaf area of each shoot (\(\text{cm}^2\)); \(N\): total leaf number of each shoot.

Fig. 3. The total leaf area of a shoot \(A_{\text{shoot}}\) is proportional to the product of foliage length \(L_f\) and width \(W_f\), as predicted by eqn (4). Each closed circle indicates an individual shoot. See Fig. 2B for the definition of foliage length and width. The blue lines show OLS (ordinary least squares) regression lines \((R^2 > 0.994)\). See Table 2 for the regression results.
The length-times-width equation for shoot leaf area

Table 2. Results of the regression analyses (OLS: ordinary least squares; SMA: standardized major axis). All regressions are significant (P < 1.0 × 10⁻⁵ for all cases).

| Y = a + bX | Type | Mgk | Cac | Prs | Udj | Fas |
|------------|------|-----|-----|-----|-----|-----|
| Y          |      |     |     |     |     |     |
| Lshoot     | OLS  | a   | 1.492 | 117.352 | 7.904 | -2.109 | -90.461 |
|            | b    | 0.546 | 0.543 | 0.519 | 0.562 | 0.652 |
|            | R²   | 0.997 | 0.996 | 0.996 | 0.997 | 0.994 |
| Wshoot     | SMA  | a   | -1.135 | -1.758 | -1.620 | -0.565 | -0.065 |
|            | b    | -0.350 | -0.502 | -0.603 | -0.199 | -0.598 |
|            | R²   | 0.964 | 0.932 | 0.947 | 0.957 | 0.968 |
| Wshoot     | OLS  | a   | 3.084 | 2.841 | 3.654 | 3.964 | 3.111 |
|            | b    | 0.963 | 0.930 | 0.946 | 0.956 | 0.967 |
|            | R²   | 0.976 | 0.957 | 0.966 | 0.951 | 0.944 |
| Wshoot     | SMA  | a   | -0.402 | -0.635 | -0.687 | -0.228 | -0.657 |
|            | b    | 3.141 | 2.943 | 3.754 | 3.132 | 3.162 |
|            | R²   | 0.964 | 0.932 | 0.947 | 0.957 | 0.968 |
| Nshoot     | OLS  | a   | 0.742 | 1.853 | 0.830 | 0.333 | 0.103 |
|            | b    | 2.325 | 1.443 | 1.865 | 1.980 | 3.137 |
|            | R²   | 0.963 | 0.857 | 0.946 | 0.855 | 0.922 |
| Nshoot     | SMA  | a   | 0.711 | 1.747 | 0.785 | 0.271 | -0.013 |
|            | b    | 2.368 | 1.555 | 1.916 | 2.136 | 3.263 |
|            | R²   | 0.964 | 0.861 | 0.948 | 0.859 | 0.925 |
| Nshoot     | OLS  | a   | 24.144 | 420.913 | 33.972 | -4.077 | -97.621 |
|            | b    | 0.630 | 0.369 | 0.637 | 0.690 | 0.712 |
|            | R²   | 0.980 | 0.976 | 0.987 | 0.996 | 0.989 |
| Nshoot     | SMA  | a   | 0.111 | 0.796 | 0.137 | -0.029 | -0.065 |
|            | b    | 1.605 | 1.080 | 1.390 | 1.288 | 1.997 |
|            | R²   | 0.977 | 0.896 | 0.962 | 0.871 | 0.943 |
| Nshoot     | OLS  | a   | 1.092 | 0.758 | 1.109 | 1.193 | 1.221 |
|            | b    | 0.994 | 0.981 | 0.991 | 0.992 | 0.993 |
| Nshoot     | SMA  | a   | 1.163 | - | -0.799 | 0.121 | 1.514 |
|            | b    | 0.648 | - | 0.643 | 0.663 | 0.798 |
|            | R²   | 0.989 | - | 0.992 | 0.992 | 0.992 |

Mgk: Magnolia kobus; Cac: Cardiocrinum cordatum; Prs: Prunus sargentii; Udj: Ulmus davidiana var. japonica; Fas: Fallopia sachalinensis.

For the other species (i.e. small, medium and large shoots were intentionally selected). Because healthy shoots were selected based solely on their sizes, both shaded and well-lit shoots were sampled for trees. For herbaceous species (Cardiocrinum and Fallopia), all shoots (ramets) within the same species grew in similar environments in their natural habitats. Cardiocrinum were sampled in partially shaded forest understories or small gaps and Fallopia were sampled in open clearings. For Cardiocrinum, leaf sizes were measured non-destructively in situ (see below). For the other species, shoots were harvested using pruning scissors or a long-reach pruner, sometimes with the aid of a stepladder. Immediately after sampling, shoots were stored in closed plastic bags with wet paper towels to avoid desiccation. Scanning (described below) was conducted within the same sampling day.

Leaf size measurements

Leaf length (Lshoot) is defined as the length of the leaf lamina, measured from the lamina tip to the point at which the lamina attaches to the petiole. Leaf width (Wshoot) is defined as the maximum lamina width perpendicular to the midvein. Individual leaf area (Aleaf) is defined as the area of one side of each lamina (John et al., 2017). For Cardiocrinum, we measured Lleaf and Wleaf of all leaves on each stem using a
measuring tape in situ. Then, $A_{\text{leaf}}$ for this species was estimated using the following equation: individual leaf area = 0.7169 (leaf length × width) (Koyama et al., 2012). For the other species, the harvested leaves were scanned using flatbed digital scanners (LiDE 210, Canon, Tokyo, Japan, 400 dpi; or 400-SCN025, Sanwa Supply, Okayama, Japan, 600 dpi). The sizes ($L_{\text{leaf}}$, $W_{\text{leaf}}$, $A_{\text{leaf}}$) of each leaf were measured using ImageJ v.1.50i or 1.53a (Schneider et al., 2012). For Cardiocrinum, both reproductive (large bolting plants) and vegetative shoots (rosettes) were sampled to cover the natural size range of this species, and the flower buds on top of Cardiocrinum stems were excluded as leaves. No reproductive organs were found among the sampled shoots of the other species. Some large shoots of Prunus and Ulmus trees, and most of the shoots of the erect herb Fallopia, were still elongating at the time of harvesting (June–August). For these shoots, only leaves of which laminae were unfolded (even when they were young and still expanding) were counted and measured; small folded immature leaves or leaf primordia near or at the shoot apical meristem were excluded as leaves. Among large shoots of Fallopia, small leaves were occasionally found on small lateral shoots that were branched from the main stem. These small lateral shoots were not measured because we focused on a single stem in this study. The total amount of those immature and lateral leaves was small compared to the total amount of leaves on the main stem.

All statistical analyses were performed with the statistical software R v.4.1.0 (R Core Team, 2021) and the packages cowplot (Wilke, 2016), ggplot2 (Wickham, 2016), gridExtra (Auguie, 2017) and smatr (Warton et al., 2012). Following Warton et al. (2006), ordinary least squares (OLS) and/or standardized major axis (SMA) regression analyses were performed for each relationship. OLS lines were fitted to predict variable $Y$ (e.g. $A_{\text{shoot}}$) from $X$ (e.g. $L_{\text{f}} \times W_{\text{f}}$) with the R function lm. SMA lines were fitted to determine the mutual allometric relationship between two variables (e.g. foliage length vs. width) with the sma function of the package smatr. The $R^2$ values of the OLS lines reported in this article were adjusted.

RESULTS

For all species investigated, the foliage length-times-width equation (eqn 4) explains $A_{\text{shoot}}$ with high accuracy ($R^2 > 0.994$ for all species; Fig. 3; Table 2). As predicted by
Eqns (6) and (7), $A_{\text{shoot}}$ can also be predicted as an allometric equation of maximum leaf length (i.e. foliage width $W_f$; Fig. 4; Table 2) or maximum leaf width alone (Fig. 5; Table 2), though with less accuracy (OLS: $R^2 = 0.930–0.976$; SMA: $0.932–0.977$). The allometric relationship between foliage width and length (eqn 5) was also supported ($R^2 = 0.905–0.960$; Fig. 6; Table 2). As expected, the scaling exponent $\beta$ was $>1$, and the value of $\beta$ varied greatly among the species (Table 2).

As predicted by eqn (9), $A_{\text{shoot}}$ is expressed as a power function of the total number of leaves on that shoot ($N$) with the SMA regression exponents $>1$ (Fig. 7; Table 2), though for this relationship substantial deviations from the regression lines ($R^2 = 0.859–0.964$; Table 2) were observed in the region for $N \leq 3$ ($\log_{10} N \leq 0.48$). This is especially evident when $N = 1$, in which case $A_{\text{shoot}}$ is represented by only a single leaf, and as $N$ increases, the values of $A_{\text{shoot}}$ become stable as they are calculated as the sum of many leaves. The present data also reconfirm all previously known empirical relationships found by Sun et al. [eqn (8); $R^2 > 0.976$; Fig. 8; Table 2], by Heerema–Span–Teobaldelli et al. [eqn (12); OLS: $R^2 = 0.871–0.977$; SMA: $R^2 = 0.874–0.977$; Fig. 9; Table 2] and by Lopes–Pinto [eqn (13); $R^2 > 0.981$; Fig. 10; Table 2]. The present data also reconfirm the leaf-level relationships that individual leaf area is proportional to the product of its lamina length and width [eqn (2); $R^2 > 0.989$; Table 2].

**DISCUSSION**

**Leaf vs. shoot elongation**

The structure of a shoot, including size variation and arrangement of leaves, determines the light-harvesting efficiency of plants (Givnish, 1984; Valladares and Brites, 2004; Pearcy et al., 2005; Smith et al., 2017; Olson et al., 2018; Koyama et al., 2020; Iwabe et al., 2021). If a shoot is to minimize the cost of current light harvesting, the optimal solution derived by Givnish (1982) is to have a single large leaf with no investment in the stem (i.e. no stem elongation). Why does a shoot have multiple leaves instead of a single large leaf? There are mutually non-exclusive explanations for the benefit of producing multi-leaved stems rather than single-leaved stems. First, plants are subject to competition with neighbours (Givnish, 1982; Anten, 2016), and existing leaves will be gradually shaded by neighbouring plants in the future. Under competition, plants should continuously elongate their
stems and produce new leaves in better-lit positions (Koyama and Kikuzawa, 2009; Anten, 2016; Koyama et al., 2020). Therefore, a shoot has at least two functions in terms of light capture: current light harvesting and space acquisition, the latter of which contributes to future light harvesting (Yagi and Kikuzawa, 1999; Sterck et al., 2005; Laurans and Vincent, 2016; Koyama et al., 2020). Differentiation of short vs. long shoots can be considered as a continuum of a strategy along the trade-off between these two functions (Yagi and Kikuzawa, 1999). In the present dataset, the exponent \( \beta \) was >1 [eqn (5); Table 2], indicating that larger foliage had a larger foliage length relative to its foliage width, as expected because larger foliage consists of more leaves than smaller foliage (Fig. 7). This phenomenon is called geometric dissimilitude and it can be considered as a shift in strategy along size variation (Niklas, 1994; Okie, 2013). These results are consistent with the observation that long shoots are specialized for space acquisition whereas short shoots are specialized for light capture, and there is a continuous shift between these two extremes (Yagi and Kikuzawa, 1999). Second, larger leaves produce a thicker boundary layer that reduces heat and gas exchange (Schuepp, 1993; Xu et al., 2009); therefore, larger leaves are subject to greater heat stress (Vogel, 2009). Having compound leaves that consist of multiple leaflets instead of simple large leaves can effectively reduce the boundary layer resistance (Gurevitch and Schuepp, 1990; Xu et al., 2009). At the level of individual leaves, Schrader et al. (2021) demonstrated that the length-times-width equation (eqn 2) is valid for compound leaves. However, at the shoot level, leaf shape (e.g. simple vs. compound) may also affect the leaf–shoot allometric relationship (Yang et al., 2009). Therefore, the scaling relationships may also be affected by the leaf shape, which is in turn is affected by the environment (Royer et al., 2005; Xu et al., 2009). Third, Kleiman and Aarssen (2007) suggested that producing more leaves, instead of fewer but larger ones, is more beneficial because it allows stems to have more buds and eventually leads to greater lateral growth and higher plasticity of allocation between growth and reproduction. Fourth, for a given limit on the total leaf area of a shoot, larger leaves incur a disproportionately greater cost of supporting tissues (Niinemets et al., 2007; Shi et al., 2020). Fifth, if a plant has many leaves, then the feeding or attacking efficiency of herbivores or pathogens may be reduced (Brown et al., 1991). Altogether, the observed variation of \( \beta \) across the five species may reflect these multiple compounding factors. Therefore, further investigations on species with different leaf shapes (such as compound leaves), leaf
sizes, leafing intensities and environments (including herbivores and pathogens) are needed.

In this study, we intentionally ignored the 3D arrangement of foliage and instead considered the 2D structure of foliage as being analogous to a single large leaf (Fig. 2B). By doing so, our length-times-width equation successfully predicted $A_{\text{shoot}}$ with high accuracy without considering any details of the actual foliage structure other than size. The simplification applied in this study is in contrast to existing models, which consider the 3D arrangement of leaves, such as phyllotaxis (Valladares and Brites, 2004; Smith et al., 2017), internode length (Meng et al., 2013), stem inclination angle (Meng et al., 2013), and the resultant light interception and within-shoot self-shading (Valladares and Brites, 2004; Koyama and Kikuzawa, 2010; Smith et al., 2017; Olson et al., 2018). Our model does not consider stem traits, such as cross-sectional area (Brouat et al., 1998; Yan et al., 2013; Smith et al., 2017; Lehnebach et al., 2018; Sun et al., 2019a,b, 2020; Fajardo et al., 2020), length-to-diameter ratio (Xiang et al., 2009a, Levinnois et al., 2021), conduit size, which determines hydraulic efficiency (Savage et al., 2010; Chen et al., 2012; Fan et al., 2017; Trueba et al., 2019; Olson et al., 2020; Bortolami et al., 2021; Levinnois et al., 2021), stem mechanical properties (Brouat and McKey, 2001; Chen et al., 2009; Trueba et al., 2016; Fan et al., 2017; Olson et al., 2018; Baer et al., 2021; Levinnois et al., 2021) or the associated stem construction costs (Yang et al., 2010; Givnish, 2020). Nonetheless, because our model focuses only on a population of leaf laminas, it is not mutually exclusive to the previous models. Instead, the geometric property of foliage can be incorporated to improve the previous models, which do not consider the within-shoot size variation of individual leaves.

**Limitations of the model**

The product of leaf lamina length and width can predict individual leaf area, and this relationship holds for diverse taxa and for different growth conditions, without considering the underlying leaf structures such as venation (Blonder et al., 2020; Kawai and Okada, 2020), lobation (Schuepp, 1993; Kus and Karsai, 2020), lamina folding (Fleck et al., 2003; Deguchi and Koyama, 2020), epidermal features (Maslova et al., 2021) and internal mesophyll structures (Oguchi et al., 2005), all of

![Log–log linear (allometric) relationship between the total leaf area of a shoot ($A_{\text{shoot}}$) and the total number of leaves on the shoot ($N$). The regression slopes correspond to $\alpha$ in eqn (9). Each closed circle indicates one individual shoot. The red lines show the SMA (standardized major axis) regression lines ($R^2 = 0.859–0.964$). See Table 2 for the regression results.](image.png)
which are known to differ among angiosperm species and under different environmental conditions. The consistency of the shoot-level results among eudicots, Magnoliids and monocots obtained herein may imply that the present results may also be generalized across angiosperms, as is the case for individual leaves. However, because our aim was to propose and test a new model as a starting point, we chose only five typical temperate woody and herbaceous species. In general, leaf–shoot allometric relationships are affected by climate or altitude (Westoby and Wright, 2003; Sun et al., 2006, 2019a; Xiang et al., 2009a, b, 2010; Zhu et al., 2019), as well as by leaf habit (i.e. deciduous vs. evergreen) (Brouat et al., 1998; Yang et al., 2008, 2009; Milla, 2009; Zhu et al., 2019; Fajardo et al., 2020). Therefore, it remains unclear whether the present results can be applied to different situations, including other species from extreme climates or different life forms, such as evergreen conifers. Additionally, our model does not consider compound leaves. At the level of individual leaves, a recent study demonstrated that the length-times-width equation (eqn 2) is valid for both simple and compound leaves (Schrader et al., 2021). However, at the level of shoots, leaf shape may also affect the leaf–shoot allometric relationship (Yang et al., 2009). Therefore, more comprehensive datasets that include a diversity of leaf forms are needed to validate our model. Furthermore, our model does not consider the reproductive organs. The scaling relationships between reproductive organs and shoot size has long been recognized (Chen et al., 2009; Scott and Aarsen, 2013; Miranda et al., 2019), and the existence of reproductive organs also alters scaling relationship among vegetative organs (Fajardo et al., 2020). Therefore, future studies are needed to elucidate whether the simple relationship found in the present study is affected by the existence of reproductive organs.

CONCLUSIONS

Based on the geometric properties of foliage, we proposed the ‘foliage length-times-width equation’ that accurately predicts the total leaf area of a shoot. The model unifies several previously established empirical relationships into a single theory. We also demonstrated that the total leaf area of a shoot can also be predicted by maximum individual leaf lamina length or width alone. The dataset of five species from diverse taxa generally supported the model predictions, though deviations from the model were also observed. More comprehensive datasets that include a diversity of species are needed to test the generality of our model in future studies.

Fig. 8. The total leaf area of a shoot ($A_{\text{shoot}}$) is proportional to the product of the maximum individual leaf area and the number of leaves on the shoot ($N$), as predicted by eqn (8). Each closed circle indicates one individual shoot. The blue lines show the OLS (ordinary least squares) regression lines ($R^2 > 0.976$).
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APPENDIX

Derivation of eqn (8)
\[
\begin{align*}
\text{mean (} L_{\text{leaf}} \text{)} & \propto \text{max (} L_{\text{leaf}} \text{)} \\
\text{mean (} W_{\text{leaf}} \text{)} & \propto \text{max (} W_{\text{leaf}} \text{)}
\end{align*}
\] (14)

By taking the product of both sides of the two lines in eqn (14), and using eqn (2), we obtained:

\[
\text{mean (} A_{\text{leaf}} \text{)} \propto \text{max (} A_{\text{leaf}} \text{)}
\] (15)

In deriving eqn (15), we assumed that the leaf that has maximum (or mean) length within each shoot also has the maximum (or mean) width in the same shoot. By multiplying both sides of eqn (15) by the total number of leaves on each shoot \((N)\), we obtained:

\[
N \cdot \text{mean (} A_{\text{leaf}} \text{)} \propto N \cdot \text{max (} A_{\text{leaf}} \text{)}
\] (16)

Because the left-hand-side of eqn (16) is \(A_{\text{shoot}}\), we obtained eqn (8).

**Derivation of eqn (9)**

In this section, we assume that lamina length and width of an individual leaf are approximately proportional to each other (Ogawa et al., 1995), and that individual leaf area can be predicted as the quadratic function of either leaf length or width alone (Teobaldelli et al., 2019a, b):

\[
A_{\text{leaf}} \propto (L_{\text{leaf}})^2
\] (17)

Equation (17) can also be used to predict the maximum \(A_{\text{leaf}}\) within each shoot:

\[
\text{max (} A_{\text{leaf}} \text{)} \propto \left[ \text{max (} L_{\text{leaf}} \text{)} \right]^2
\] (18)

By multiplying both sides of eqn (18) by the total number of leaves on each shoot \((N)\), we obtained:

\[
N \cdot \text{max (} A_{\text{leaf}} \text{)} \propto N \cdot \left[ \text{max (} L_{\text{leaf}} \text{)} \right]^2
\] (19)

By combining eqns (8) and (19), we obtained:

\[
A_{\text{shoot}} \propto N \cdot \left[ \text{max (} L_{\text{leaf}} \text{)} \right]^2
\] (20)

By using our definition of \(W_f\) (eqn 3), eqn (20) can be rewritten as follows:

\[
A_{\text{shoot}} \propto N \cdot W_f^2
\] (21)

By combining eqns (6) and (21), we obtained:

\[
W_f^{\beta+1} \propto N \cdot W_f^2
\] (22)

Equation (22) can be solved for \(W_f\):

\[
W_f \propto N^{\frac{1}{\beta+1}}
\] (23)

By substituting eqn (23) into eqn (6), we obtained:

\[
A_{\text{shoot}} \propto W_f^{\beta+1} \propto N^{\alpha}
\] (24)

**Derivation of eqn (10)**

Equation (9) can be solved for \(N_f\):

\[
N \propto (A_{\text{shoot}})^{\frac{1}{\alpha}}
\] (25)

Using eqn (25), we obtained:

\[
\frac{A_{\text{shoot}}}{N} \propto (A_{\text{shoot}})^{1 - \frac{1}{\alpha}} \equiv (A_{\text{shoot}})^{\lambda}
\] (26)

**Derivation of eqn (11)**

By combining eqns (5) and (23), we obtained:

\[
L_f \propto W_f^\beta \propto N^\frac{\beta}{\beta+1}
\] (27)

By substituting eqn (27) into eqn (4), we obtained:

\[
A_{\text{shoot}} \propto W_f \cdot N^\frac{\beta}{\beta+1} \equiv W_f \cdot N^\gamma
\] (28)

**Derivation of eqn (13)**

When different-sized foliage sets are affine to each other, the maximum leaf size relative to the mean value and the minimum leaf size relative to the mean value would be constants, independent of foliage size. This leads to the following relationship:

\[
\text{mean (} A_{\text{leaf}} \text{)} \propto \text{min (} A_{\text{leaf}} \text{)}
\] (29)

By dividing both sides of eqns (15) and (29) by 2, and adding them, we obtained:

\[
\text{mean (} A_{\text{leaf}} \text{)} \propto \frac{\text{min (} A_{\text{leaf}} \text{)} + \text{max (} A_{\text{leaf}} \text{)}}{2}
\] (30)

By multiplying both sides of eqn (30) by \(N\), we obtained eqn (13).