Leaf shape influences the scaling of leaf dry mass vs. area: a test case using bamboos

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RESEARCH PAPER

Leaf shape influences the scaling of leaf dry mass vs. area: a test case using bamboos

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Abstract

• *Key message* A highly significant and positive scaling relationship between bamboo leaf dry mass and leaf surface area was observed; leaf shape (here, represented by the quotient of leaf width and length) had a significant influence on the scaling exponent of leaf dry mass vs. area.

• *Context* The scaling of leaf dry mass vs. leaf area is important for understanding how plants effectively intercept sunlight and invest carbon to do so. However, comparatively few, if any, studies have focused on whether leaf shape influences this scaling relationship.

• *Aims* In order to explore the effects of leaf shape on the scaling relationship between leaf dry mass and area, we examined 101 species, varieties, forms, and cultivars of bamboo growing in China and identified the relationship between the scaling exponent of leaf dry mass vs. area and leaf shape. This taxon was used because its leaf shape is conserved across species and, therefore, easily quantified.

• *Methods* Ten thousand and forty-five leaves from 101 bamboo species, varieties, forms, and cultivars growing in China were collected, and leaf dry mass, the quotient of leaf width and length, leaf area, and leaf dry mass per unit area were measured. The effect of leaf shape that can be easily quantified using the quotient of leaf width and length on the relevant and ecologically important scaling exponents was explored using this data base.

• *Results* Leaf dry mass and area differed significantly across bamboo genera, and even within the same genus. However, a statistically robust log-log linear and positive scaling relationship was observed for mass and area with a 1.115 scaling exponent (95% CI = 1.107, 1.122; $r^2 = 0.907$). Leaf shape had a significant influence on the numerical values of the scaling exponent of leaf dry mass vs. area. When the median of the quotient of leaf width and length was below 0.125, the numerical value of the scaling exponent increased with increasing quotient of leaf width and length. When the median of the quotient of leaf width and length was above 0.125, the scaling exponent numerically decreased toward 1.0.

• *Conclusion* We show, for the first time, that a significant relationship exists between leaf shape and the numerical values of scaling exponents governing the scaling of leaf dry mass with respect to leaf area. In addition, we show that with the quotient of

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leaf width and length increasing mean LMA increases, which implies a negative correlation between mean LMA and the estimated exponent of leaf dry mass vs. area for the grouped data based on the sorted quotients of leaf width and length.

1 Introduction

The relationship between plants and their environment has always been a focus of ecological investigation since the time of Darwin (1871; see Shipley 1995; Poorter and Evans 1998; Díaz and Cabido 2001; Norby and Luo 2004; Shipley et al. 2006), and such plant-environment interactions can result in adaptive plant strategies reflected in morphology, anatomy, and physiology (Niklas 1999, 2000; Díaz and Cabido 2001; Vendramini et al. 2002). Plant functional traits are core attributes that are closely associated with plant dispersal, colonization, survival, growth, and mortality, and can notably affect forest ecosystem functions and reflect the response of plants to environmental changes (Liu and Ma 2015). To simplify the concept, Violle et al. (2007) have proposed that functional traits should be defined as any phenotypic expression that indirectly affects the fitness of a species. Similarly, McIntyre et al. (1999) have defined plant traits as characteristics that are easy to observe or measure (e.g., plant height, leaf size, etc.) and that objectively express a plant's adaptability to its external environment (see also Niinemets et al. 2007).

Among the most widely studied adaptive traits of plants are those associated with photosynthetic leaves, both functional (e.g., gas exchange, photosynthetic rates, etc.) and structural traits (e.g., dry mass, lamina area, etc.) (see for example Niklas 1999, 2000; Gurevitch 1992; Morecroft and Roberts 1999; Violle et al. 2007; Zhang et al. 2012). Leaf traits mainly include lifespan (Reich et al. 1991, 1992; Wright and Westoby 2002), lamina length and width, leaf dry weight, and leaf shape (e.g., the quotient of leaf width and length) (Reich et al. 1998; Aranda et al. 2004; Poorter et al. 2009; Shi et al. 2019a, b). Many of these functional traits reflect the adaptability of plants to cope with different environmental gradients, and provide easily measured and observed links between various environmental factors and metabolic activity (Ellsworth and Reich 1993; Schulze et al. 1994; Reich et al. 1998; Kikuzawa and Ackerly 2002; Wright et al. 2004a). Leaf dry mass per unit area (LMA) or its reciprocal specific leaf area (SLA) is a critical trait that is closely associated with plant growth rates, reproductive strategies, and lifespan (Wright et al. 2004b; Poorter et al. 2009). LMA can also be approximately regarded as the product of leaf thickness and bulk tissue density (Witkowski and Lamont 1991; Lin et al. 2018). Higher LMA implies larger investment in mass per unit area, and as a consequence it could reduce the hazards of wind, frost, and snow to leaves (Wittenbach et al. 1980; Wright and Westoby 2002). If the

increase in surface area is proportional to that of dry mass (which means that the scaling exponent of leaf dry mass vs. area is equal to unity), LMA is a constant. However, numerous data sets have demonstrated that leaf area, on average, fails to keep pace with leaf mass for many broad-leaved species (Milla and Reich 2007; Niklas et al. 2007; Huang et al. 2019), i.e., the scaling exponent for leaf surface area vs. dry mass is less than 1.0. This phenomenon has been referred to as "diminishing returns" (Niklas et al. 2007).

Surprisingly, little or nothing is known about the effect of leaf shape on the scaling relationships pertaining to leaf mass and area. This gap in our knowledge is surprising considering that leaf shape is an important factor influencing the fitness of plants (Tsukaya 2005) because it can influence how total leaf area is distributed within a canopy (Stewart and Dwyer 1999) as well as other phenomena such as transpiration and photosynthesis. Leaf shape can also provide insights into developmental processes. For example, asymmetric (unequal) growth of the lamina (Calvo-Alvarado et al. 2008) is often closely related to phenotypic plasticity during leaf development (Mùller et al. 2000; Weiner 2004). The area difference between the left and right sides of leaves might result from the influence of the aboveground architectural structures of plants on the heterogeneity of light interception for leaves in different positions (Küppers 1989; Sumida and Komiyama 1997; Wang et al. 2018). Leaf phenotypic plasticity implies that plants tend to invest more dry mass to the side of a leaf facing the sunlight rather than to the side in shade, to make plants maximize light use. Such an imbalance of dry mass investment in two sides of a leaf usually leads to leaf bilateral asymmetry (Wang et al. 2018). This further suggests that blade width, due to the asymmetric investment in dry mass, is more likely to show a large variation than blade length, which has been demonstrated by Shi et al. (2018) and Su et al. (2019). In other words, the variation in the quotient of leaf width and length needs to be considered in the investigation of leaf shape. Collectively, therefore, the scaling relationships of leaf shape, mass, and area may shed light on how leaves maintain a positive carbon balance (Niklas et al. 2009; Pan et al. 2013).

The goal of this paper is to explore the influence of leaf shape on the scaling relationship between leaf dry mass and surface area. Toward this end, bamboo species were selected because the shape of their leaves can be mathematically described with rigor using the simplified Gielis equation that can describe the shape of bamboo leaf boundary (Shi et al. 2015b, 2018; Lin et al. 2016; Su et al. 2019), and because they are one

of the most important forest resources in the world, i.e., bamboo species can provide both theoretical and practical insights. Bamboos grow in tropical, subtropical, and warm temperate regions between 46° N and 47° S. There are more than 150 genera and approximately 1300 species worldwide (Kelchner 2013; Liese and Köhl 2015; Wysocki et al. 2015). More than 500 species and 35 genera grow in China, accounting for 46% of the world's bamboo species. In addition, many cultivars of bamboo are available for study in China. Indeed, China is known as the "kingdom of bamboo" (Jiang 2007). As noted, other leaf attributes make bamboos suitable of scaling studies, i.e., their vegetative leaves are typically simple, their phyllotaxy is relatively simple, their overall shape is conserved throughout the whole subfamily (Bambusoideae), and their leaf shapes are easily described with great accuracy using the simplified Gielis equation (Shi et al. 2015b, 2018; Lin et al. 2016; Su et al. 2019). Although previous studies have focused primarily on morphological and anatomical structure (Wright et al. 2004a, 2005a, b; Niklas and Christianson 2011), most workers have largely neglected the relationship between leaf mass and area in tandem with lamina shape. Using these attributes of bamboo leaves, we address three important questions: (i) what is the relationship between the M vs. A scaling exponent and leaf shape (here, represented by the quotient of leaf width and length), (ii) what is the scaling relationship between leaf mass and area among species, and (iii) do the scaling exponents of M vs. A significantly differ across species.

2 Materials and methods

2.1 Collection sites

We collected 10,045 leaves from 101 species, varieties, forms, and cultivars of bamboo. Among them, 89 species were collected from the Nanjing Forestry University campus (118° 48′ 42″ E, 32° 04′ 34″ N) and the Baima Resource Nursery of Nanjing Forestry University (119° 07′42″E, 31° 37′55″ N), Nanjing, Jiangsu Province; eight species from Tongzi County (106° 44′–106° 57′ E, 28° 13′–28° 43′ N), Zunyi City, Guizhou Province; and four species from the Southwest Forestry University Campus (102° 45′26″E, 25° 3′44″ N), Kunming City, Yunnan Province (see Table 1 in the annex for details). The environmental factors on the Nanjing Forestry University campus and the Baima Resource Nursery of Nanjing Forestry University, both in Nanjing City, are so close that any difference due to the influence of different climate types on growth can be neglected. Nanjing belongs to the southeast monsoon climate, with a mean annual precipitation of 1058 mm and a mean annual temperature of 15 °C. Minimum daily temperature is − 13 °C, and the maximum daily temperature is 40 °C. Tongzi County belongs to the plateau under subtropical monsoon climate, with a mean annual precipitation of 994 mm and a mean annual temperature of 14 °C. The minimum daily temperature is − 5 °C, and the maximum daily temperature is 36 °C. Kunming belongs to the south subtropical monsoon climate, with a mean annual precipitation of 979 mm and a mean annual temperature of 15 °C. The minimum daily temperature is − 7 °C, and the maximum daily temperature is 31.3 °C. These climate data are based on the 1980–2018 climate records from China Climate Data Online (www.data.cma.cn). The above daily mean, minimum, and maximum temperatures are the means of the past 39 years.

2.2 Collection and measurement protocols

Leaves from a total of 101 species, varieties, forms, and cultivars of bamboo were collected. Table 1 (in the annex) provides the genera and species according to *Flora of China* (Wu et al. 2006 and *Bamboos of the World* (Ohrnberger 1999)), collection sites, and sampling dates. Leaves were randomly collected from different locations within middle canopies without distinguishing between shade and sun leaves. Samples were gathered from at least three different healthy adult individuals that were similar in size and age. Only mature leaves were collected and processed within 10 min in the field. Leaves were placed into large sealed polyethylene bags containing wet paper to maintain moisture. The bags were stored in an ice box to prevent decomposition. Because the collection sites of most materials in Nanjing were near the laboratory, the entire processing was completed within 2 h. Approximately 100 leaves were collected from different conspecifics for each taxon and measured to ascertain leaf area, width, length, and dry mass. *W/L* and LMA were subsequently calculated.

Leaf lamina area and shape were recorded using a HP Scanjet 4850 scanner (Hewlett-Packard Company, Palo Alto, CA). The images were saved as bitmap images at a 200-dpi resolution. Adobe Photoshop (version: CC 2017) was used to obtain a new layer of the leaf edge in a black-white image (Shi et al. 2015a). The M-function (using MATLAB version ≥2009a developed by Shi et al. (2015a, 2018) and Su et al. (2019)) was used to extract the planar coordinates of the leaf edge from each black-white image; the R script developed by Su et al. (2019) was then used to calculate leaf area, length, and width. Leaves were then dried in a ventilated oven at 80 °C for at least 72 h until obtaining a constant dry mass using an electronic balance (ME204/02, Mettler Toledo Instrument (Shanghai) Co., Ltd., Shanghai, China).

All raw data of leaf length, width, surface area, fresh mass, and dry mass for the 101 data sets can be found and freely downloaded in the Dryad repository (Lin et al. 2019; see the data1 comma-delimited file therein for details).

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Table 1   Data collection information and scientific names of bamboos

Data set no.	Genus	Latin name	Collection sites	Location	Sampling date
1	*Bambusa*	*Bambusa emeiensis* L.C. Chia et H.L. Fung	Tongzi, Zunyi, Guizhou Province	106° 57′52″E, 28° 43′20″N	2018.6.17
2	*Bambusa*	*Bambusa emeiensis* "Viridiflavus"	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.23
3	*Bambusa*	*Bambusa multiplex* (Loureiro) Raeuschel ex Schultes & J.H. Schultes	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.24
4	*Bambusa*	*Bambusa multiplex* 'Alphonse-Karr'	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.27
5	*Bambusa*	*Bambusa subaequalis* H.L. Fung et C.Y. Sia	Southwest Forestry University Campus, Kunming, Yunnan Province	102° 45′26″E, 25° 3′44″N	2018.7.30
6	*Bambusa*	*Bambusa ventricosa* McClure	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.21
7	*Bashania*	*Bashania fargesii* (E.G. Camus) Keng f. et Yi	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
8	*Chimonobambusa*	*Chimonobambusa angustifolia* C.D. Chu et C.S. Chao	Baima Resource nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
9	*Chimonobambusa*	*Chimonobambusa communis* (Hsueh & T.P. Yi) T.H. Wen et Ohrnberger	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
10	*Chimonobambusa*	*Chimonobambusa marmorea* (Mitford) Makino	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.22
11	*Chimonobambusa*	*Chimonobambusa marmorea* f. *variegata* Ohwi	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.28
12	*Chimonobambusa*	*Chimonobambusa purpurea* Hsueh & T.P. Yi	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.22
13	*Chimonobambusa*	*Chimonobambusa quadrangularis* (Franceschi) Makino	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.22
14	*Chimonobambusa*	*Chimonobambusa setiformis* Wen	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
15	*Chimonobambusa*	*Chimonobambusa sichuanensis* (T.P. Yi) T.H. Wen	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.22
16	*Chimonobambusa*	*Chimonobambusa tumidissinoda* Hsueh & T.P. Yi ex Ohrnberger	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.22
17	*Chimonobambusa*	*Chimonobambusa utilis* (Keng) P.C. Keng	Tongzi, Zunyi, Guizhou Province	106° 44′25″E, 28° 17′39″N	2018.6.12
18	*Dendrocalamus*	*Dendrocalamus brandisii* (Munro) Kurz	Southwest Forestry University Campus, Kunming, Yunnan Province	102° 45′26″E, 25° 3′44″N	2018.7.30
19	*Dendrocalamus*	*Dendrocalamus latiflorus* Munro	Tongzi, Zunyi, Guizhou Province	106° 57′52″E, 28° 43′20″N	2018.6.17
20	*Dendrocalamus*	*Dendrocalamus sinicus* Chia et J.L. Sun	Southwest Forestry University Campus, Kunming, Yunnan Province	102° 45′26″E, 25° 3′44″N	2018.7.30
21	*Drepanostachyum*	*Drepanostachyum luodianense* (Yi et R.S. Wang) Keng f.	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
22	*Drepanostachyum*	*Drepanostachyum microphyllum* (Hsueh et Yi) Keng f. ex Yi	Tongzi, Zunyi, Guizhou Province	106° 57′52″E, 28° 43′20″N	2018.6.17
23	*Drepanostachyum*	*Drepanostachyum scandens* (Hsueh et W.D. Li) Keng f. ex Yi	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
24	*Fargesia*	*Fargesia alatovaginata* Yi et J.Y. Shi	Tongzi, Zunyi, Guizhou Province	106° 50′36″E, 28° 15′26″N	2018.6.16
25	*Fargesia*	*Fargesia denudata* T.P. Yi	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″ N	2018.6.4
26	*Fargesia*	*Fargesia yunnanensis* Hsueh & T.P. Yi	Southwest Forestry University Campus, Kunming, Yunnan Province	102° 45′26″E, 25° 3′44″ N	2018.7.30
27	*Hibanobambus*	*Hibanobambusa tranquillans* f. *shiroshima* H. Okamura	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.27
28	*Indocalamus*	*Indocalamus chishuiensis* Y.L. Yang et Hsueh	Tongzi, Zunyi, Guizhou Province	106° 58′50″E, 28° 13′12″N	2018.6.19
29	*Indocalamus*	*Indocalamus hirtivaginatus* H.R. Zhao & Y.L. Yang	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.24
30	*Indocalamus*	*Indocalamus tessellatus* (Munro) Keng f.	Tongzi, Zunyi, Guizhou Province	106° 58′39″E, 28° 13′51″N	2018.6.19

Table 1 (continued)

Data set no.	Genus	Latin name	Collection sites	Location	Sampling date
31	*Indosasa*	*Indosasa gigantea* (T.H. Wen) T.H. Wen	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.6.2
32	*Indosasa*	*Indosasa shibataeoides* McClure	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.21
33	*Indosasa*	*Indosasa sinica* C.D. Chu & C.S. Chao	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.30
34	*Oligostachyum*	*Oligostachyum lubricum* (Wen) Keng f.	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
35	*Oligostachyum*	*Oligostachyum oedogonatum* (Z.P. Wang et G.H. Ye) Q.F. Zheng et K.F. Huang	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
36	*Oligostachyum*	*Oligostachyum sulcatum* Z.P. Wang et G.H. Ye	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.30
37	*Phyllostachys*	*Phyllostachys arcana* f. *luteosulcata* C.D. Chu et C.S. Chao	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.23
38	*Phyllostachys*	*Phyllostachys aurea* Carrière ex Rivière & C. Rivière	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.22
39	*Phyllostachys*	*Phyllostachys aurea* f. *flavescens-inversa* (H. de Lehaie) Muroi	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
40	*Phyllostachys*	*Phyllostachys aurea* f. *koi* G.H. Lai	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
41	*Phyllostachys*	*Phyllostachys aureosulcata* McClure	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.27
42	*Phyllostachys*	*Phyllostachys aureosulcata* f. *aureocaulis* McClure	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
43	*Phyllostachys*	*Phyllostachys aureosulcata* f. *spectabilis* C.D. Chu et C.S. Cha	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.25
44	*Phyllostachys*	*Phyllostachys bambusoides* Sieb et Zucc.	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.21
45	*Phyllostachys*	*Phyllostachys bambusoides* f. *castillonis* (Mitford) Muroi	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.30
46	*Phyllostachys*	*Phyllostachys bambusoides* f. *lacrimadeae* Keng f. et Wen	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.27
47	*Phyllostachys*	*Phyllostachys bambusoides* f. *marliacea* (Makino ex I. Tsuboi) Muroi	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
48	*Phyllostachys*	*Phyllostachys bambusoides* f. *mixta* Z.P. Wang et N.X. Ma	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
49	*Phyllostachys*	*Phyllostachys bissetii* McClure	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.25
50	*Phyllostachys*	*Phyllostachys dulcis* McClure	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
51	*Phyllostachys*	*Phyllostachys edulis* (Carrière) H. de Lehaie	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.27
52	*Phyllostachys*	*Phyllostachys edulis* f. *gracilis* (Hsiung) Chao et Renv.	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.28
53	*Phyllostachys*	*Phyllostachys edulis* f. *huamaozhu* (Wen) Chao et Renv.	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
54	*Phyllostachys*	*Phyllostachys edulis* 'Kikko-chiku' G.H. Lai	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.6.2
55	*Phyllostachys*	*Phyllostachys glabrata* S.Y. Chen et C.Y. Yao	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
56	*Phyllostachys*	*Phyllostachys glauca* McClure	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.28
57	*Phyllostachys*	*Phyllostachys heteroclada* Oliver	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
58	*Phyllostachys*	*Phyllostachys heteroclada* f. *decurtata* (S.L. Chen) Wen	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
59	*Phyllostachys*	*Phyllostachys hispida* S.C. Li	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
60	*Phyllostachys*	*Phyllostachys makinoi* Hayata	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4

Table 1 (continued)

Data set no.	Genus	Latin name	Collection sites	Location	Sampling date
61	*Phyllostachys*	*Phyllostachys meyeri* McClure	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
62	*Phyllostachys*	*Phyllostachys nidularia* Munro	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.28
63	*Phyllostachys*	*Phyllostachys nigra* (Lodd. ex Lindl.) Munro	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
64	*Phyllostachys*	*Phyllostachys nigra var. henonis* (Mitford) Stapf ex Rendle	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.6.2
65	*Phyllostachys*	*Phyllostachys parvifolia* C.D. Chu *et* H.Y. Chou	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
66	*Phyllostachys*	*Phyllostachys prominens* W.Y. Xiong	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
67	*Phyllostachys*	*Phyllostachys propinqua* McClure	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.23
68	*Phyllostachys*	*Phyllostachys rivalis* H.R. Zhao et A.T. Liu	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
69	*Phyllostachys*	*Phyllostachys rutila* T.H. Wen	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
70	*Phyllostachys*	*Phyllostachys shuchengensis* S.C. Li & S.H. Wu	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
71	*Phyllostachys*	*Phyllostachys sulphurea* f. *robertii* Chao et Renv.	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
72	*Phyllostachys*	*Phyllostachys sulphurea* var. *viridis* R.A. Young	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.24
73	*Phyllostachys*	*Phyllostachys violascens* (Carrière) A. et C. Riv.	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.6.2
74	*Phyllostachys*	*Phyllostachys violascens* f. *viridisulcata* (P.X. Zhang et W.X. Huang) G.H. Lai	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
75	*Phyllostachys*	*Phyllostachys viridiglaucescens* (Carr.) A. et C. Riv.	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
76	*Phyllostachys*	*Phyllostachys vivax* f. *aureocaulis* N.X. Ma	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.30
77	*Phyllostachys*	*Phyllostachys vivax* f. *huangwenzhu* J.L. Lu.	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
78	*Phyllostachys*	*Phyllostachys vivax* 'Jintianyu'	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
79	*Pleioblastus*	*Pleioblastus amarus* (Keng) Keng f.	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
80	*Pleioblastus*	*Pleioblastus argenteostriatus* (Regel) Nakai	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.21
81	*Pleioblastus*	*Pleioblastus chino* (Franchet et Savatier) Makino	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.21
82	*Pleioblastus*	*Pleioblastus fortunei* (Van Houtte) Nakai	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.25
83	*Pleioblastus*	*Pleioblastus gozadakensis* Nakai	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
84	*Pleioblastus*	*Pleioblastus gramineus* (Bean) Nakai	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
85	*Pleioblastus*	*Pleioblastus maculatus* (McClure) C.D. Chu & C.S. Chao	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.21
86	*Pleioblastus*	*Pleioblastus oleosus* T.H. Wen	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.6.2
87	*Pleioblastus*	*Pleioblastus pygmaeus* (Miq.) Nakai	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.24
88	*Pleioblastus*	*Pleioblastus solidus* S.Y. Chen	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
89	*Pleioblastus*	*Pleioblastus sp.*	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
90	*Pleioblastus*	*Pleioblastus viridistriatus* Makino	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.21

Table 1 (continued)

Data set no.	Genus	Latin name	Collection sites	Location	Sampling date
91	*Pseudosasa*	*Pseudosasa amabilis* var. *convexa* Z.P. Wang & G.H. Ye	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.23
92	*Pseudosasa*	*Pseudosasa japonica* (Siebold & Zuccarini ex Steudel) Makino ex Nakai	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.25
93	*Pseudosasa*	*Pseudosasa japonica* var. *tsutsumiana* Yanagita	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
94	*Sasaella*	*Sasaella glabra* f. *albostriata* Muroi	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.30
95	*Sasaella*	*Sasaella kogasensis* 'Aureostriatus'	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.24
96	*Semiarundinaria*	*Semiarundinaria densiflora* (Rendle) T.H. Wen	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.23
97	*Semiarundinaria*	*Semiarundinaria fastuosa* (Mitford) Makino	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
98	*Semiarundinaria*	*Semiarundinaria sinica* T.H. Wen	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.27
99	*Sinobambusa*	*Sinobambusa tootsik* (Sieb.) Makino	Nanjing Forestry University Campus	118° 48′51″E, 32° 4′59″N	2018.5.28
100	*Sinobambusa*	*Sinobambusa tootsik* var. *luteoloalbostriata* S.H. Chen ex Z.Z. Wang	Baima Resource Nursery of Nanjing Forestry University	119° 07′42″E, 31° 37′55″N	2018.6.4
101	*Yushania*	*Yushania niitakayamensis* (Hayata) Keng f.	Tongzi, Zunyi, Guizhou Province	106° 58′50″E, 28° 13′12″N	2018.6.16

2.3 Methods

As in previous reports (Milla and Reich 2007; Niklas et al. 2007), the relationships between M and A conformed to a power law form:

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

where α (the scaling exponent) and β (the normalization constant) are parameters determined using regression protocols. The data were log-transformed to stabilize the variance:

$$\ln(M) = \ln(\beta) + \alpha \ln(M).$$

Reduced major axis (RMA) was used (Smith 2009) to obtain the estimates of the numerical values of α and β.

The following protocol was used to examine the effect of leaf shape, defined as the quotient of leaf width and length (W/L), on the scaling exponent of leaf dry mass vs. area: (i) the pooled W/L data were sorted in increasing order and divided into v quantiles, where v is an integer set at 4, 8, 12, and 16; (ii) the log-transformed data of leaf dry mass and area associated with each quantile group was regressed to obtain the estimates of the scaling exponent for each quantile; and (iii) a scatterplot of the estimates of the scaling exponent versus the medians of W/L of the v quantiles was prepared and examined. In addition, the local regression method (Cleveland and Grosse 1991) was also used to explore whether leaf shape influenced the

scaling exponent of leaf dry mass vs. area. Similarly, we also examined the influence of leaf shape on mean LMA based on the above grouped data of W/L. However, we used a linear regression rather than the local regression to reflect such an influence because the data of mean LMA vs. the median of W/L showed an apparent linear trend. The analysis of covariance was used to test whether the intercepts and slopes for the four regression lines have significant differences.

The HSD.test function in package "agricolae" (version 1.2-4) was used to compare the significance of the difference in the quotient of leaf width and length and LMA among different bamboo species. The statistical software R was used to draw figures and perform statistical analyses (R Core Team 2015).

3 Results

LMA and W/L differed significantly among different genera and among different bamboo species within the same genus (see the data2 and data3 comma-delimited files in Lin et al. 2019). Mean LMA ranged from 20.1 g/m² (data set 21: *Drepanostachyum luodianense*) to 73.7 g/m² (data set 92: *Pseudosasa japonica*). Among species from the same genus (e.g., *Phyllostachys*), LMA varied, often significantly (see blue boxes in Fig. 1a). Mean leaf W/L ranged from 0.07213 (species 84: *Pleioblastus gramineus*) to 0.22813 (species 19: *Dendrocalamus latiflorus*) (Fig. 1b). However, the W/L

Fig. 1 Comparison of leaf dry mass per unit area (**a**) and that of leaf width/length quotient (**b**) among 101 bamboo taxa (Poaceae: Bambusoideae). The red boxes represent the observations of 6 *Bambusa* species; the green boxes represent the observations of 10 *Chimonobambusa* species; the blue boxes represent the observations of 42 *Phyllostachys* species, varieties, forms, and cultivars; the light blue boxes represent the observations of 12 *Pleioblastus* species; and the gray boxes represent the observations of the remaining species of genera having less than five species
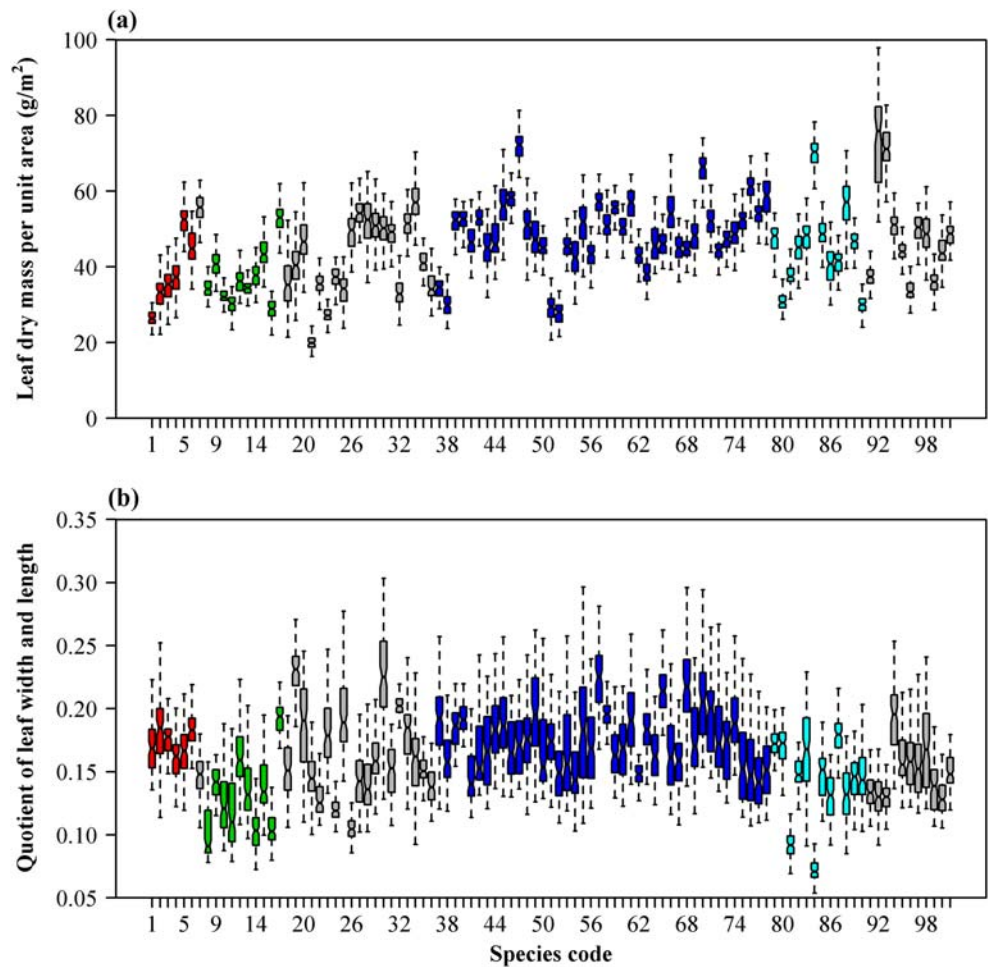
observed for some species belonging to different genera were statistically indistinguishable (see the data3 comma-delimited file in Lin et al. 2019). Figure 2a shows the distribution of the leaf *W/L* for the pooled data; Fig. 2b shows the normality test using a Q − Q plot.

There was a highly significant and positive relationship between leaf dry mass and area among 10,045 leaves from 101 species, varieties, forms, and cultivars of bamboo that we will refer to as 101 data sets for simplicity below (Fig. 3). Leaf mass increased disproportionately

Fig. 2 The density of the leaf width and length quotient of the pooled data for 101 bamboo taxa with the corresponding normal Q − Q plot
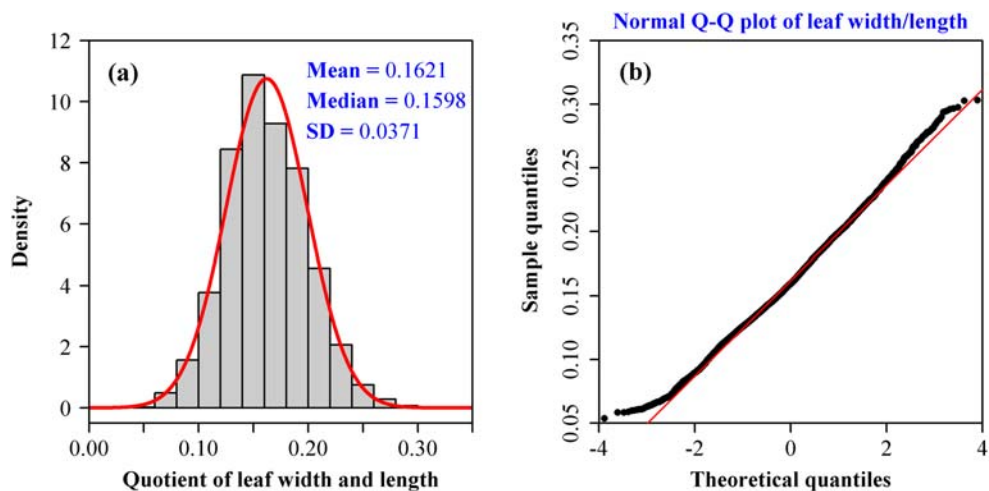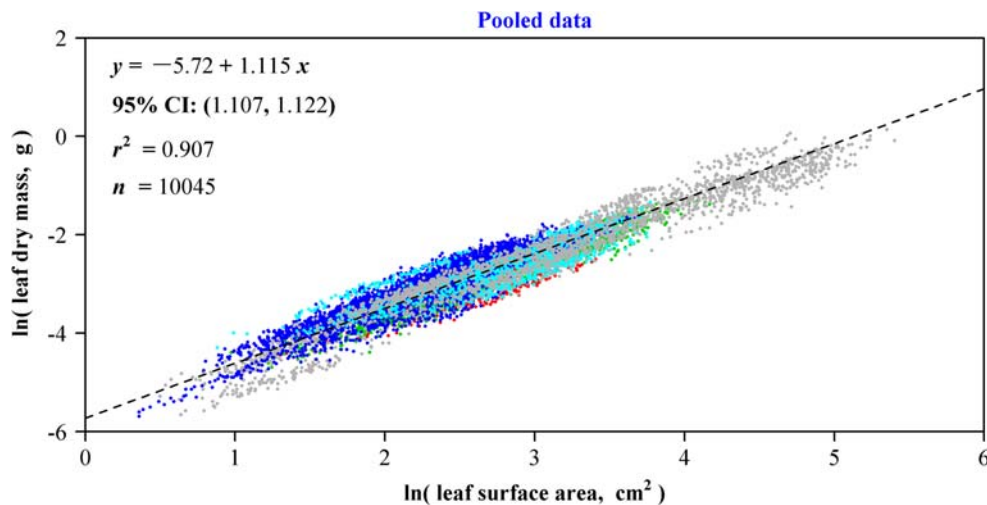
Fig. 3 The scaling relationship between leaf dry mass and leaf surface area. The small point represents the observations of the log-transformed leaf dry mass vs. the log-transformed leaf area, and the straight line represents the fitted regression line based on the ordinary least-squares method. CI represents the 95% confidence interval of slope of the fitted linear equation; r^2 represents the coefficient of determination that is used to indicate the goodness of fit; and n represents the sample size, namely total of sampled leaves. The red points represent the observations of 6 *Bambusa* species; the green points represent the observations of 10 *Chimonobambusa* species; the blue points represent the observations of 42 *Phyllostachys* species, varieties, forms, and cultivars; the light blue points represent the observations of 12 *Pleioblastus* species; and the gray points represent the observations of the remaining species of genera having less than five species

with respect to increasing leaf area. At the subfamily level, the scaling exponent (α) was estimated to be 1.115 (95% CI = 1.107, 1.122; $r^2 = 0.907$; $n = 10,045$ bamboo leaves) (Fig. 3). At the individual species level, the 95% CIs of the 83 data sets (i.e., the data of dry mass vs. area

of 83 species) did not include 1.0 (all lower bounds exceeded 1.0), whereas the 95% CIs of 18 species included 1.0 (see the data4 comma-delimited file in Lin et al. 2019), i.e., we observed the phenomenon referred to as "diminishing returns" (Niklas et al. 2007).

Fig. 4 Effect of the leaf width/ length quotient on the estimate of the scaling exponent of leaf dry mass vs. leaf area. **a** 4 quantiles, **b** 8 quantiles, **c** 12 quantiles, and **d** 16 quantiles. The blue open circles with bars represent the estimates of the scaling exponent of M vs. A with their standard deviations, and the red curve represents the predicted values by the local regression
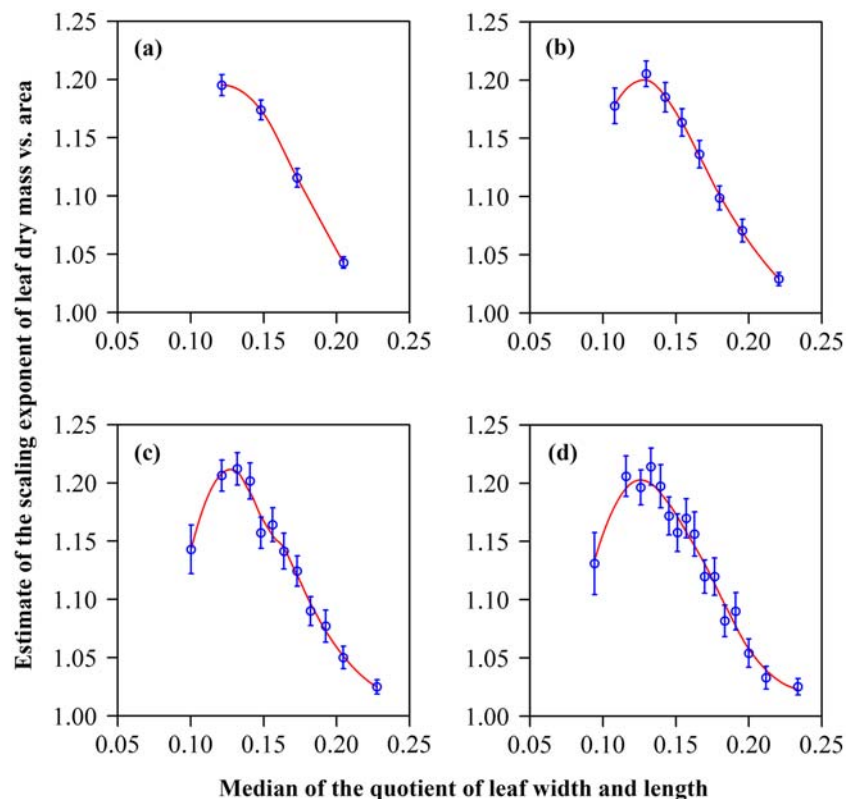
Finally, and perhaps most importantly, there was a similar response curve of the scaling exponent to median leaf shape (as defined by *W/L*) for the different quantile groups (Fig. 4). When the median was less than 0.125, scaling exponents increased with increasing median leaf *W/L*. When the median exceeded 0.125, scaling exponents decreased with increasing *W/L*. Since the median leaf *W/L* of most bamboo leaves exceeds 0.125, the scaling exponents on average tended to decrease for wider leaves, and the asymptotic value of the slope approached 1.0.

Although there was a large variability in LMA for each group, the slope was demonstrated to be significant for the linear regression of mean LMA vs. the median of *W/L* (*P* < 0.05 for each of the four groups of data; Fig. 5). Analysis showed that there were no significant differences in intercepts and slopes among the four regression lines. That is, the influence of leaf shape on mean LMA is not affected by the grouping number based on the sorted quotients of leaf width and length.
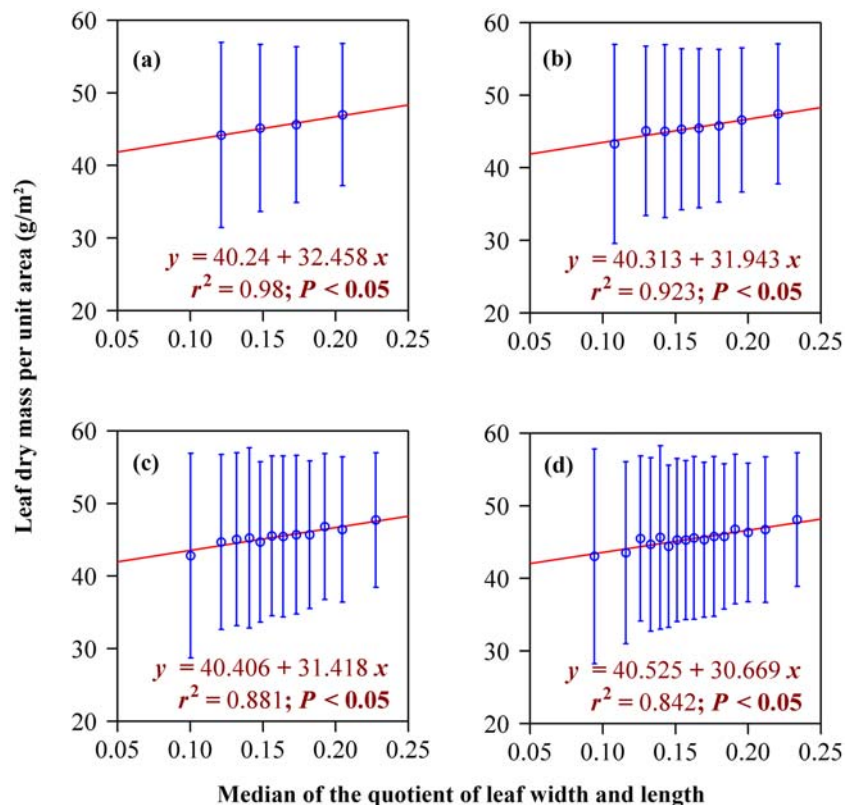
4 Discussion

Functional trait analyses have identified LMA as one of the most important leaf traits affecting leaf photosynthetic rates, plant growth rates and yield, reproductive strategies, and leaf

structure and lifespan (Reich et al. 1998; Poorter et al. 2009). However, to the best of our knowledge, few studies have investigated whether this important trait is correlated with leaf shape (as defined, here, simply by the quotient of leaf width and leaf length). Our data show that leaf shape is an important variable that influences the scaling of leaf mass with respect to leaf area. This phenomenology (and the context in which it is reported here) is discussed below.

Although it is well known that the values of LMA and density in broad-leaved species are greater in more arid environments (Niinemets 2001) and that long-lived leaves have higher LMA than short-lived leaves (Mediavilla et al. 2001), the data presented here show that these relationships may also be correlated with leaf shape. For example, sun leaves have higher LMA than shade leaves and, in those species with lobed leaves, sun leaves tend to have more deeply lobed leaves than shade leaves. Similarly, on the worldwide global basis, a strong negative relationship between LMA and rainfall has been reported for evergreen shrubs and trees (Wright and Westoby 2002). Asner et al. (2011) report that the total LMA range of plants in humid tropical forests is 22.2–307.6 g/m^2, among which median LMAs are 61.7 g/m^2 for vines, 88.9 g/m^2 for lianas, 107.2 g/m^2 for trees, 121.2 g/m^2 for palms, and 134.3 g/m^2 for hemi-epiphytes (based on top-canopy leaf samples from 2873 individuals in 57 sites across the neotropics, Australasia, Caribbean and Pacific Islands). In

Fig. 5 Effect of the leaf width/length quotient on mean LMA. **a** 4 quantiles, **b** 8 quantiles, **c** 12 quantiles, and **d** 16 quantiles. The blue open circles with bars represent the LMAs with their standard deviations, and the red straight line represents the predicted values by the linear regression

Graph (a): $y = 40.24 + 32.458\,x$; $r^2 = 0.98$; $P < 0.05$

Graph (b): $y = 40.313 + 31.943\,x$; $r^2 = 0.923$; $P < 0.05$

Graph (c): $y = 40.406 + 31.418\,x$; $r^2 = 0.881$; $P < 0.05$

Graph (d): $y = 40.525 + 30.669\,x$; $r^2 = 0.842$; $P < 0.05$

Leaf dry mass per unit area (g/m^2)

Median of the quotient of leaf width and length

the case of bamboo species, our study identified median LMAs that are relatively smaller compared to those reported in previous studies (e.g., Asner et al. 2011), ranging from 20 g/m^2 (data set 21: *D. luodianense*) to 76 g/m^2 (data set 92: *P. japonica*). Most bamboos are distributed from temperate to tropical areas where climatic conditions, especially temperature and humidity, are fairly different from other biomes, such that they have evolved a series of leaf shapes with different *W/L* values.

It is important to point out that LMA is not uniform throughout a canopy. It can change as a function of leaf position, tree age, soil nutrient availability, and the light environment (Abrams and Kubiske 1990). This plasticity as well as ontogenetic changes must be taken into account when drawing ecological inferences from LMA data (Aranda et al. 2004; McKown et al. 2012). Our data imply that these relationships may be correlated also with leaf shape.

Across the plant kingdom, leaf area varies from less than 1 mm^2 to greater than 1 m^2 (Díaz et al. 2016). Wright et al. (2017) characterized worldwide patterns in leaf size by compiling a leaf size data set for 7670 species from 682 nonagricultural sites worldwide. They concluded that large-leaved species predominate in wet, hot, and sunny environments, while small-leaved species are found in harsh conditions such as high latitudes, high elevations, nutrient poor, and hot arid conditions. In our study, we show that the leaves of bamboo species grown in Yunnan and Guizhou are relatively larger than the leaves from bamboos grown in Nanjing. We find that leaf size and LMA are not closely related, which is consistent with some previous reports (Ackerly and Reich 1999; Fonseca et al. 2000).

Pan et al. (2013) investigated a wide range of scaling exponents and the variation in leaf dry mass (*M*) to lamina area (*A*) across different altitudes (exponents ranged from 0.859 to 1.299). In our study, scaling exponents ranged from 1.002 to 1.315, with a mean scaling exponent of 1.106. This is consistent with prior studies (Niklas et al. 2007, 2009; Price and Enquist 2007), particularly with previous studies of bamboo leaves (Lin et al. 2018). The variations in the *M* vs. *A* scaling relationship likely reflects evolutionary trade-offs among morphological and anatomical traits shared by all vascular plants (Niklas et al. 2007). Several studies have shown that the increase of leaf dry mass does not result in a proportional increase in leaf area (Niklas et al. 2007; Milla and Reich 2007). However, Pan et al. (2013) analyzed the scaling relationships between leaf dry mass and leaf area for 121 vascular plant species along an altitudinal gradient in a subtropical monsoon forest, and report that the scaling exponent increases with altitude, changing from less than 1.0 at low altitudes to greater than 1.0 at high altitude. Likewise, Niklas et al. (2007) report scaling exponents with numerical values in excess of one for some species functional groups. Thus, the generality of "diminishing returns" must be questioned. In this

study, mean LMA increased with the median of *W/L* increasing, which exhibited a converse trend relative to the scaling exponent of leaf dry mass vs. area (Figs. 4 and 5). The correlation coefficients between mean LMA and the scaling exponent of leaf dry mass vs. area for any groups (based on the 4, 8, 12, and 16 quantiles) were equal to −0.97, −0.83, −0.68, and −0.69, respectively; the corresponding *P* values were all smaller than 0.05, which implies a significant negative correlation between them. The result confirms to our recent report on 12 species of vines (Shi et al. 2020). There was a negative correlation between the median of the LMA values and the scaling exponent of leaf dry mass vs. area for the vines (−0.47; *P* < 0.05). Bamboo leaves have typical parallel veins. Because leaf vein pattern, shape, size, and density interact with each other (Sack et al. 2012; Runions et al. 2017), it deserves a further investigation on why a smaller quotient of leaf width and length has generated a smaller LMA as shown in Fig. 5. It might result from a scaling relationship between leaf density and *W/L*. For a narrower bamboo leaf, we hypothesize that it might only require fewer veins to achieve the transportation of water and nutrients and support leaf physical structures, which consequently results in a lower LMA.

Unfortunately, the influence of leaf shape on LMA has been largely ignored in most comparisons of LMA among different species or different individuals of the same species. In this study, we have shown that leaf shape can affect (or at least is correlated with) the numerical values of the scaling exponents of leaf dry mass vs. area (and thus LMA). Thus, in theory, significant differences in LMA may exist even between two closely related species possessing different leaf shapes. Likewise, it is possible for two unrelated species to have similar or even identical LMA provided that they have leaves with the same or similar shapes. Leaf shape is known to vary more across environments compared to leaf size or LMA (Thomas and Bazzaz 1996; McDonald et al. 2003), perhaps because leaf shape is determined less by genetic factors (Pien et al. 2001; Bensmihen et al. 2008) and more by environmental factors (Niinemets 2001; Nicotra et al. 2011; Pan et al. 2013; Sun et al. 2017). Early leaf development can be profoundly influenced by abiotic factors such as water availability. For example, water stress decreases the acidity of cell walls, which can negatively affect leaf growth (Bacon et al. 1998; Fan and Neumann 2004). Indeed, our field observations indicate that bamboo leaf width is affected by water availability such that leaf shape becomes narrower under conditions of water stress, whereas in areas with abundant rainfall, the lamina of bamboos is wider. For example, in the case of *P. gramineus*, a species distributed in temperate and subtropical zones, the mean leaf width/length quotient equals 0.07213, whereas for *D. latiflorus*, a species that is widely distributed in subtropical and tropical zones, the mean leaf width/length quotient equals 0.22813.

Although the lanceolate shape of bamboo leaves is fairly similar (Shi et al. 2015b; Lin et al. 2016), the leaf width and length quotient across different species demonstrably differs, and, the narrower the lamina, the greater the estimated scaling exponent of the leaf dry mass vs. leaf area relationship (Fig. 4). Therefore, the dry mass of narrower bamboo leaves increases disproportionately with increasing leaf area, which implies that the leaf carbon content per unit area is increasing with increasing leaf area. The opposite is true for broader leaves. Previous researches show that plants tend to produce large and flat leaves in wet and warm regions, while plants with small and dissected leaves were commonly found in cool and dry regions (Gates et al. 1968; Parkhurst and Loucks 1972; Smith and Nobel 1977; Fonseca et al. 2000; McDonald et al. 2003; Nicotra et al. 2011). In this regard, it is noteworthy that bamboo species with slender leaves are usually distributed in northern subtropical areas and are prone to disproportionately allocate more dry mass to lamina and are thus likely to tolerate low temperatures and droughts. Leaf shape appears to be an important factor even when data from different species are pooled. For example, a previous study shows that the scaling exponent of leaf fresh mass vs. area is 1.147 for the pooled data of 11 bamboo species ($r^2 = 0.99$, Lin et al. 2018; see also Huang et al. 2019). This finding can be explained by the fact that all bamboo plants have a similar leaf shape regardless of the differences in the quotients of leaf width and length (Shi et al. 2018, 2019b). However, for 12 species of Rosaceae, the scaling relationship between leaf dry mass and area for the pooled data of 3857 leaves was weak (i.e., $r^2 = 0.738$; Yu et al. 2019), presumably because of the large variation in leaf shape within this family.

This study used bamboo leaves and regarded all bamboo leaves. Actually, we regarded all leaves from these 101 bamboo taxa as one regardless of the interspecific differences, because bamboo leaf shapes have showed a similarity that could be described by the simplified Gielis equation only with two parameters (Shi et al. 2015b; Lin et al. 2016). The variation in leaf shape for Bambusoideae is mainly reflected by the difference in the quotient of leaf width and length. We believe that the conclusions from this study may apply to other broad-leaved plants with more complex leaf shapes. The conclusions can hold true when the users correctly define blade width and length. Liu et al. (2019) studied the influence of leaf shape on the scaling exponent of leaf dry mass vs. surface area of *Ginkgo biloba* L. They also used the quotient of leaf width and length as the representative of leaf shape; leaf width was first defined as the distance between the two farthest ends of the fan-shaped blade; leaf length was then defined as the maximum distance between the junction (of leaf petiole and the blade) and a point on the blade edge that could make the straight line through them be perpendicular to the straight line through the two farthest ends of the fan-shaped blade. Three hundred sixty leaves from 10 trees of the same cultivar were divided into two groups according to the sorted quotients of leaf width and length. Liu et al. (2019) also found that the

estimated scaling exponent of leaf dry mass vs. area of the group with broader leaves is significantly smaller than that of another group with narrower leaves, which is in accordance with our result. In other words, for a single species, if there is a large variation in leaf *W/L*, the current conclusions could apply to the grouped leaves based on the sorted *W/L*. Whether the conclusions apply to other plant taxa (e.g., angiosperms with more teeth, lobes, and dissections) and the leaflets of compound leaves is worthy of a further investigation.

5 Conclusions

In summary, we have shown that a significant and a potentially ecologically important relationship exists between leaf shape and the scaling of leaf dry mass vs. leaf area (which, in our data set, generally complies with the hypothesis of "diminishing returns"). It is reasonable to speculate that similar leaf shape-dependent relationships may exist for species with more elaborate lamina morphologies. We selected bamboo leaves to illustrate the potential of this approach because the shapes of bamboo leaves are easily quantified (using, for example, the simplified Gielis equation). Future research will be required to validate or refute the speculation that leaf shape influences (or at least is correlated with leaf area indices), but it is clear that the effects of leaf shape on leaf functional traits should not be neglected when considering the leaf economic spectrum.

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