



Original article

Functional relationships of leafing intensity to plant height, growth form and leaf habit

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ABSTRACT

Leafing intensity, *i.e.* the number of leaves per unit of stem volume or mass, is a common developmental correlate of leaf size. However, the ecological significance and the functional implications of variation in leafing intensity, other than its relation to leaf size, are unknown. Here, we explore its relationships with plant height, growth form, leaf size, and leaf habit to test a series of corollaries derived from the leafing intensity premium hypothesis. Volume-based leafing intensities and plant heights were recorded for 109 woody species from the subtropical evergreen broadleaf forests of eastern China. In addition, we compiled leafing intensity data from published literature, and combined it with our data to form a 398 species dataset, to test for differences of leafing intensity between plant growth forms (*i.e.* herbaceous and woody) and leaf habits (*i.e.* deciduous and evergreens). Leafing intensity was negatively correlated with plant height and individual leaf mass. Volume-based leafing intensities were significantly higher in herbaceous species than in woody species, and also higher in deciduous than in evergreen woody species. In conclusion, leafing intensity relates strongly to plant height, growth form, leaf size, and leaf habit in directions generally in accordance to the leafing intensity premium hypothesis. These results can be interpreted in terms of the evolution of adaptive strategies involving response to herbivory, competitive ability for light and reproductive economy.

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1. Introduction

Leaf size variation among species is extremely wide and its interpretation has been the subject of extensive research (Parkhurst and Loucks, 1972; Givnish, 1987; Bragg and Westoby, 2002; Ackerly et al., 2002; Niklas et al., 2007; Niinemets et al., 2007). Previous explanations of inter-specific leaf size variation include herbivory pressures (Brown and Lawton, 1991; Coley and Barone, 1996; Moles and Westoby, 2000; Haukioja and Koricheva, 2000; Miller et al., 2006; Hanley et al., 2007), and ecophysiological adaptations associated with optimizing photosynthesis, gas exchange, energy flux and/or water use efficiency (Parkhurst and Loucks, 1972; Givnish, 1987; Bragg and Westoby, 2002; Milla and Reich, 2011; Niinemets et al., 2007). These interpretations account for why climate and other abiotic variables are generally correlated with leaf size variation; *e.g.* heat, cold, drought and high-radiation stresses all tend to

select for relatively small leaves, while leaf size is generally larger in wet, shady, and nutrient-rich habitats (Givnish, 1987; Ackerly et al., 2002; Westoby and Wright, 2003).

Leaf size variation can also be accounted for by its coordinated evolution with other plant traits (Westoby and Wright, 2003; Milla and Reich, 2011). In particular, leaf size is developmentally and ecologically coordinated with the size of the shoot on which it is attached (Westoby and Wright, 2003; Sun et al., 2006). Also, the same total leaf area for a given size of shoot can be built out of many small leaves or with fewer larger leaves. Accordingly, leaf size may partly be a trade-off of leaf number per unit shoot size (the latter referred to as 'leafing intensity') in plants (Kleiman and Aarssen, 2007; Yang et al., 2008; Milla, 2009; Whitman and Aarssen, 2010). In fact, leafing intensity, being defined as the number of leaves per unit of stem volume or mass, has been shown to be tightly related to leaf size variation in a number of empirical studies (Kleiman and Aarssen, 2007; Yang et al., 2008; Ogawa, 2008; Milla, 2009; Whitman and Aarssen, 2010). However, the wider ecological importance of leafing intensity and its relationships to other plant traits, remain largely unstudied.

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Predictions for leafing intensity patterns associated with growth form or leaf habit may be connected with susceptibility to herbivory. Plants with many leaves on a given shoot size (high leafing intensity) may spread out the risk of herbivore attack and some leaves may remain undiscovered and hence unaffected by herbivorous insects (Mooney et al., 1983; Brown and Lawton, 1991). Since leaves of herbaceous and deciduous plants, as compared to woody and evergreens, respectively, have generally less chemical and physical defense (e.g. soft leaves), they are more prone to be attacked by herbivores (Mooney et al., 1983; Coley and Barone, 1996; Brown and Lawton, 1991; Mole, 1994; Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Haukioja and Koricheva, 2000; Hanley et al., 2007). Accordingly, we might expect leafing intensity – as an adaptation to herbivory – to be higher in herbaceous and deciduous plants than in woody and evergreen plants.

Leafing intensity might also be expected to show relationships with plant height. Since each leaf is normally associated with an axillary meristem (lateral bud), high leafing intensity necessarily represents a relatively large number of meristems ('bud bank') per unit shoot size (Kleiman and Aarssen, 2007). Relatively tall plants are particularly adapted to competition for light, typically through strong apical dominance at the expense of reduced lateral growth, where relatively few axillary meristems are deployed for branching (Geber, 1990; Aarssen, 1995; Bonser and Aarssen, 1996; Cline, 1997; Olejniczak, 2001). Rather than producing a large number of small leaves (and hence a large bud bank), therefore taller species may be better served by producing larger (and hence fewer) leaves, because—elevated on a tall plant—these may serve well in shading competitors (Bragg and Westoby, 2002; Falster and Westoby, 2003, 2005). Smaller species, on the other hand, may benefit more from having a relatively large bud bank per unit shoot size (conferred through a relatively high leafing intensity), thus providing more axillary meristems that are available for deployment as reproductive units (Rubinstein and Nagao, 1976; Geber, 1990; Olejniczak, 2001; Vesik and Westoby, 2004). In addition, high leafing intensity (hence a large bud 'bank') for understory small plants may permit greater plasticity in meristem allocation to vegetative growth, and thus enhanced capacity to adjust shoot production and placement in response to changes in light availability (Rubinstein and Nagao, 1976; Bonser and Aarssen, 1996). Based on this line of reasoning therefore, we might expect leafing intensity to be negatively correlated with plant height.

In the present study, the above predictions were tested making use of two different datasets. First, we tested whether leafing intensity is negatively correlated with plant height in a dataset of leafing intensities and plant height for 109 woody species in the subtropical evergreen broadleaf forests in eastern China. Second, we compiled leafing intensity data from published literature (Yang et al., 2008; Milla, 2009; Whitman and Aarssen, 2010), and combined it with our unpublished data to form a 398 species dataset. This larger dataset was used to test for differences of leafing intensity between plant forms (i.e. herbaceous and woody) and leaf habits (i.e. deciduous and evergreens). Our specific objectives were to test the hypotheses that leafing intensity is: (i) negatively correlated with plant height and leaf size; (ii) higher in herbaceous than in woody species; and (iii) higher for deciduous species than for evergreens.

2. Materials and methods

2.1. Study sites and vegetation

The species used to build this dataset were located in the Tiantong National Forest Park (29°41'–50'N, 121°36'–52'E) and

surrounding area, situated on the lower eastern extension of the Siming Mountain, Zhejiang province, Eastern China. The highest peak in this area is at 653 m above sea level, while most other relief is in the range of 70–300 m. The area has a typical monsoon climate with a hot, humid summer and a drier cold winter (Yan et al., 2006). This region supports evergreen broad-leaved forests (EBLF). Regionally, mature and secondary EBLF usually occur in mesophytic habitats. Ravines and mountain bases are dominated by deciduous broad-leaved species, mixed with evergreens in the understory. Outside of the park, virtually all vegetation is secondary (Yan et al., 2006).

2.2. Species, twig and leaf collection and measurement

In order to screen an ample number of woody species and reduce intra-specific variation of plant traits within-species existing in different habitats, we chose mature and secondary EBLFs, and secondary shrubs in mesophytic habitats, and evergreen and deciduous mixed forests in highland and ravine habitats. In total, we established 31 plots. A total of 109 species was sampled, belonging to 33 families and 69 genera, including 1233 individual trees and shrubs (Appendix 1). For each species, 3–15 individuals were sampled. The same species from different habitats were pooled together to get species means for leafing intensity, and then divided into two groups, i.e. evergreens and deciduous. For standardization purposes, plant height data for each species was the maximum plant height of that species observed in our 31 study plots.

In each plot, the woody species having greater than five individuals present were selected. For each species, at least three randomly selected individuals were marked in each plot, and then twig and leaf samples were collected from those marked plants, in July and August 2008. For each individual plant, five branches were cut from the four directions and the upper position of plant crowns. In the field, the first (current) year twigs being already fully expanded were separated from the branch immediately after being collected according to the terminal set of internodes. Those first year shoots were defined here as twigs. From each branch, one twig without apparent leaf loss or damage was chosen, stored in a plastic zip-loc bag and kept cool until returned to the laboratory for later measurement, usually within 12 h. In the laboratory, the leaf and stem in each twig were separated and the leaf number was counted. Then twig length and twig diameters at the mid point along the length were measured using an electronic vernier caliper, accurate to 0.1 mm. Twig cross-sectional area was calculated from diameter. At the same time, twig and leaf samples were dried in a 75 °C oven for 48 h to determine twig and leaf dry mass.

We followed Kleiman and Aarssen's (2007) method to define leafing intensity, i.e. leaf number per unit of twig mass and/or volume, respectively. Volume-based leafing intensity, calculated as the number of leaves supported on a twig divided by the twig stem volume. Stem volume was assumed to be approximate to a cylinder shape, with mid-point stem diameter as the cylinder width and stem length as the cylinder height.

2.3. Compilation of literature data

Data on leafing intensities were obtained from Milla (2009) and Whitman and Aarssen (2010). In the Milla (2009) dataset, since leafing intensity for 57 species derived from Kleiman and Aarssen (2007) and Westoby and Wright (2003) were corrected from the raw data, we thus deleted these species. Totally, together with 109 new species in this study (China dataset), we built the complete 398 species database. In this new dataset (composite dataset), species was categorized as 163 herbaceous and 235 woody plants,

and 115 evergreen and 283 deciduous plants, by referring to source papers.

2.4. Data analyses

A hierarchical ANOVA was carried out for leafing intensity to decompose variance into components between-species, within-species and within-individual. We fitted a general linear model to the variance of trait across three scales nested one into another (i.e. nested ANOVA with random effects) in the increasing order of twig, individual and species, by using a restricted maximum likelihood (REML) method in the 'lme' function of R (version 2.11.1). In this procedure, a variance component analysis was performed on this model using the 'varcomp' function of R (R-Development Core Team, 2009). Afterward, variables were averaged arithmetically in individuals and then within-species. If a species was present in several sites in the leafing intensity dataset, data were averaged among sites.

The relationships between leafing intensity and each of plant height and leaf size were described by a mathematical equation of the type $y = bx^a$, linearized under the form $\log(y) = \log(b) + a \log(x)$, x and y being the dimensions of the two parts considered. The value of the slope determines whether the relationship is isometric ($a = 1$, no change of form among species) or allometric. The term b is the y -intercept of the relationship. Model type II regression analysis was used to estimate the parameters of the equations. Slopes of the relationship were calculated as standardized major axis (SMA) (Falster et al., 2006), which is also known as reduced major axis (RMA) (Sokal and Rohlf, 1995). Type II regression procedures were carried out using (S)MATR (Version 2.0, Falster et al. 2006, <http://www.bio.mq.edu.au/ecology/SMATR/>). Confidence intervals for individual regression slopes were calculated following Pitman (1939). Tests for heterogeneity of regression slopes and calculation of common slopes where homogeneity of slopes was demonstrated were carried out through re-sampling and permutation procedures (Warton and Weber, 2002; Warton et al., 2006). When slopes did not differ among successional stages, differences in the y -intercept were tested by ANOVA (and post hoc Tukey tests where appropriate) available in (S)MATR. In this procedure, cross-species regressions were fitted separately for each leaf habit in both the China and the composite datasets, while for growth form regression being only conducted in the composite dataset, due to the unavailability of data for herbaceous plants in the China dataset. The regression relationship between leafing intensity and plant height was carried out in the China dataset.

In addition, the two-way ANOVA was used to determine whether there were significant effects of growth form and leaf habit on each response (volume- and mass-based leafing intensities) for the composite dataset. Growth form and leaf habit were considered as fixed effects. Further, in order to confirm whether these relations are consistent between the composite and China datasets, the one-way ANOVA was used to determine the effects of leaf habit on the volume- and mass-based leafing intensities. In this case, the leaf habit was included as fixed effect. After this, Bonferroni's test was used to detect difference of leafing intensity between herbaceous and woody, and between deciduous and evergreens. All statistical tests were considered significant at the $P < 0.05$ level.

Finally, to check the effects of evolutionary divergence on leafing intensity, we carried out phylogenetic signal analyses on these traits. The phylogenetic inertia in the evolution of mass- and volume-based leafing intensity was calculated by running the Analysis Of Traits (AOT) module of Phylocom (Webb et al., 2006). We found that the evolution of leafing intensity does not show phylogenetic signal (see details in Appendix 2). Given this result, together with the absence of phylogenetic signal in leaf size in the

few studies performed so far (e.g. Ackerly and Reich, 1999; Whitman and Aarssen, 2010), we considered it unnecessary to perform independent contrasts.

3. Results

3.1. Variability of leafing intensity in China dataset

Among 109 woody species, the variation for mass- and volume-based leafing intensity was 54- and 40-fold, respectively (Appendix 1). The hierarchical ANOVA showed that, over 90% of this variation was accounted for by differences among species. Variance absorbed by among individual variation was 2.27% and 4.98% for mass- and volume-based leafing intensity respectively, while inter-twigs differences were comparatively smaller (0.13 for mass-based leafing intensity and 1.03% for volume-based leafing intensity).

3.2. Relationship between leafing intensity and plant height

In the China dataset, both mass- and volume-based leafing intensities were negatively correlated with plant height. This was consistent regardless of the species being evergreen or deciduous (Fig. 1). There was no difference in the regression slope between the two leaf habits for both mass- and volume-based leafing intensities.

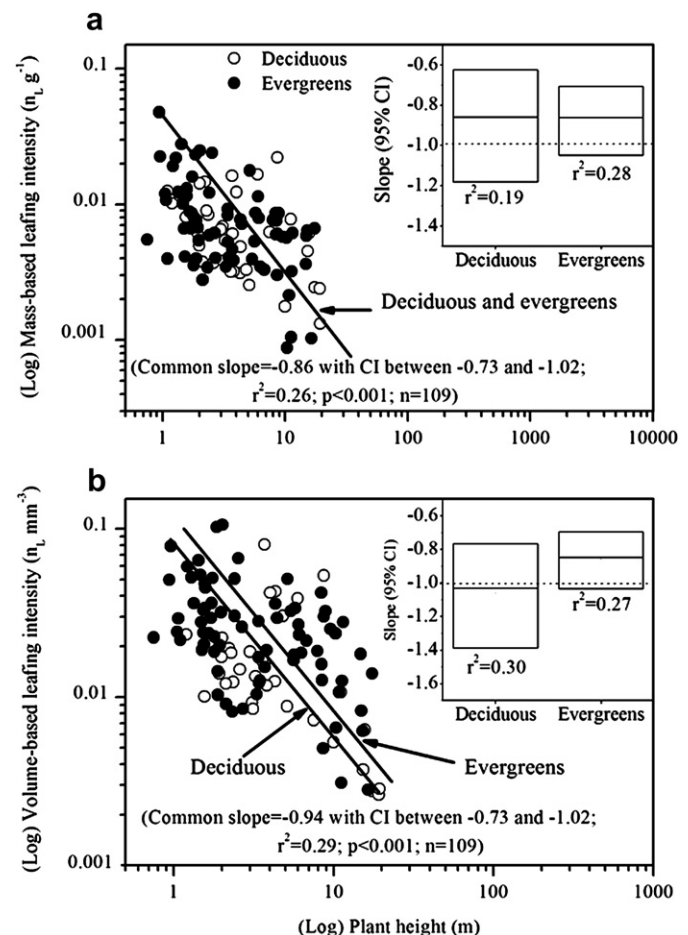


Fig. 1. Scaling relationship between (log) plant height and each of (log) mass-based (a) and (log) volume-based (b) leafing intensity for 34 deciduous and 75 evergreen woody plants in eastern China. The lines are the reduced major axis regression curves. The inserted box-plot in each panel shows regression slopes, 95% confidence intervals, and determinate coefficients (r^2) for each of the two relationships. The dotted line in each box-plot indicates isometric position (slope = -1).

Table 1

Summary of SMA regression parameters for the scaling relationships between leaf mass and each of mass-based leafing intensity (LI_M) and volume-based leafing intensity (LI_V) for plant species representing contrasting leaf habits and growth forms in both the China dataset and the composite dataset.

	Dataset	Leaf habit and growth form	n	r^2	Slope	95% confidence intervals (CIs)
Leaf mass – LI_M	China	Evergreens	75	0.91***	–0.95	(–1.02, –0.89)
		Deciduous	34	0.60***	–1.08	(–1.35, –0.86)
	Composite	Evergreens	115	0.87***	–1.20	(–1.28, –1.12)
		Deciduous	156	0.87***	–1.17	(–1.24, –1.11)
Leaf mass – LI_V	China	Evergreens	75	0.22*	–0.94	(–1.08, –0.81)
		Deciduous	34	0.62***	–1.29	(–1.80, –0.93)
	Composite	Evergreens	115	0.61***	–0.81	(–0.91, –0.72)
		Deciduous	161	0.56***	–0.91	(–1.00, –0.82)
Leaf mass – LI_M	Composite	Herbaceous	36	0.64***	–1.24	(–1.53, –1.00)
Leaf mass – LI_V		Woody	235	0.85***	–1.16	(–1.22, –1.10)

*** means $P < 0.001$; * means $P < 0.05$.

Also, the regression slopes did not differ from -1.0 , indicating a negative isometric relationship between leafing intensity and plant height (Fig. 1). Since the slopes were homogeneous (not statistically different, $P > 0.05$), there was common regression slope for each of the two relationships (Fig. 1). The intercept of regression line for mass-based leafing intensity was the same for evergreens and deciduous (Fig. 1a). On the other hand, significant shifts ($P < 0.001$) in the intercept were found for volume-based leafing intensity between leaf habits: evergreens $>$ deciduous (Fig. 1b).

3.3. Relationship between leaf size and leafing intensity

Leaf mass (referring to leaf size) was negatively correlated with both mass- and volume-based leafing intensities across plant species representing contrasting leaf habits and growth forms in both the China and the composite datasets. The leaf size-number trade-off was isometric in the China dataset, but allometric in the composite dataset (Table 1). For leaf habit comparison, the

regression slopes were homogenous between leaf habits in the two datasets. Thus, as shown in Fig. 2, their common slope can be calculated for each relationship. Notably, significant shifts of y-intercept were not found for any relationship. In the comparison of growth forms, the regression slope was homogenous for relationships between leaf mass and mass-based leafing intensity. Also, there was no significant y-intercept shift in the relationship between leaf mass and mass-based leafing intensity (Fig. 3a). In contrast, the regression slope was heterogeneous for the relationship between leaf mass- and volume-based leafing intensity (Fig. 3b).

3.4. Comparisons of leafing intensity between growth forms and leaf habits

For the composite dataset, two-way ANOVA's showed that mass-based leafing intensity was significantly affected by the leaf habit, woodiness and their interaction, while volume-based leafing

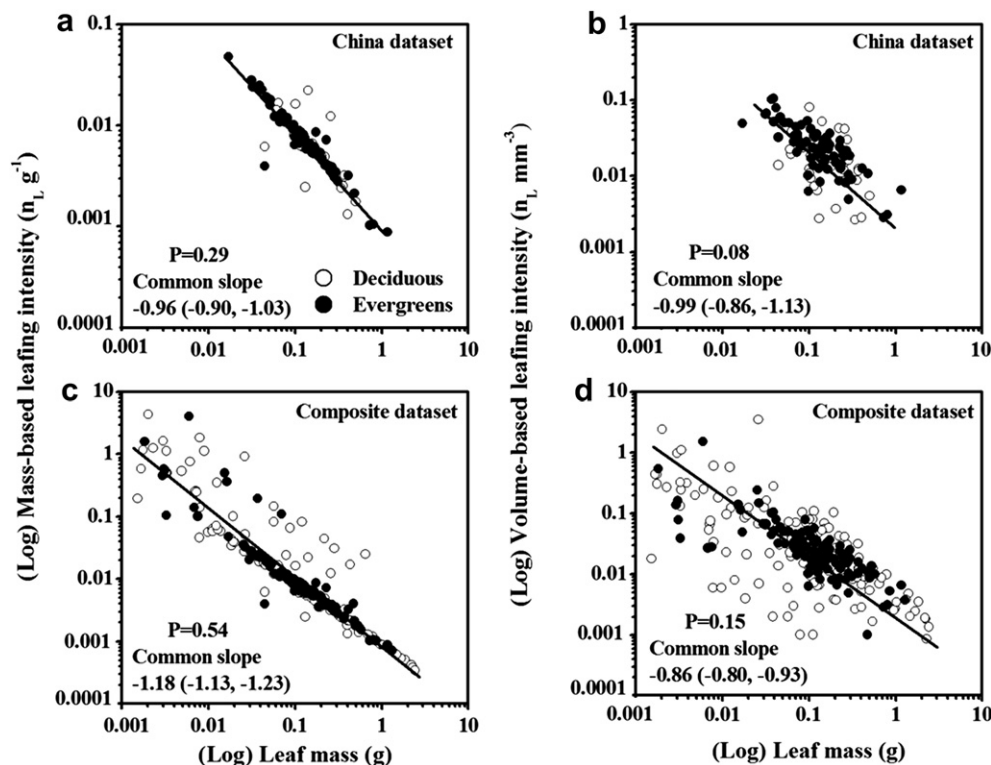


Fig. 2. Scaling relationships between (log) leaf mass and (log) leafing intensities for the plants with different leaf habits in both the China dataset (a and b) and the composite dataset (c and d). Fig. 2a and c is the mass-based leafing intensity; Fig. 2b and d is the volume-based leafing intensity. Among four cases, individual slopes are non-heterogeneous, and therefore the common slope with its 95% CI is shown in the respective figure. As no significant difference in the y-intercepts is found between evergreens and deciduous, only the common slopes' lines are shown.

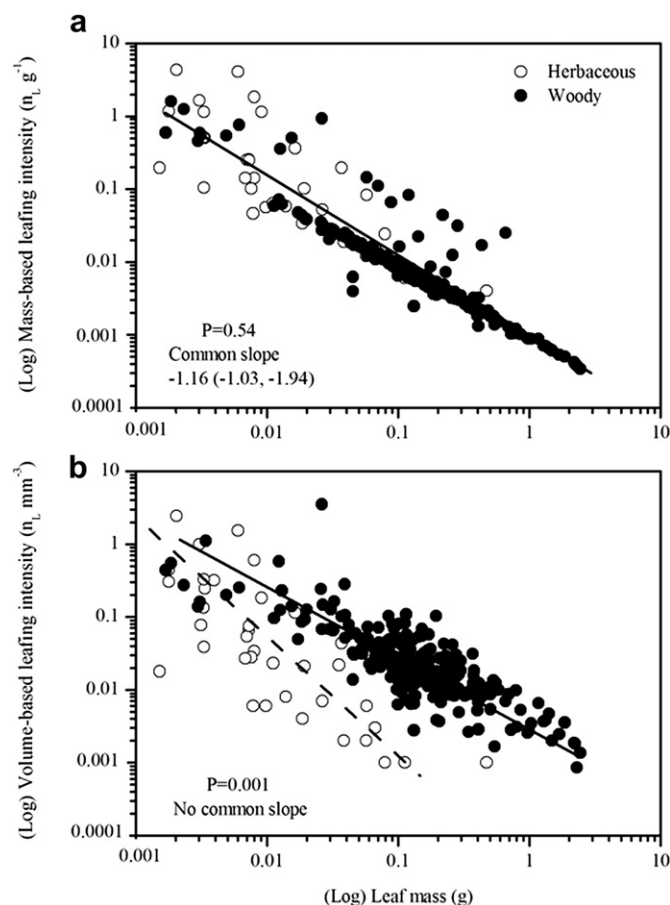


Fig. 3. Scaling relationships between (log) leaf mass and each of (a) (log) mass-based leafing intensity and (b) volume-based leafing intensity for the plants with different growth forms in the composite dataset. For (a), individual slopes are non-heterogeneous, and no significant difference in the y-intercepts is found between herbaceous and woody species, therefore the common slope with its 95% CI and the common slopes' lines are shown. For (b), different regression lines are shown given that individual slopes are heterogeneous between herbaceous and woody species.

intensity was only affected by plant woodiness (Table 2). Mass-based leafing intensity was significantly higher in herbaceous plants than in woody plants (Fig. 4a), and this was also the case for volume-based leafing intensity (Fig. 4d). Regarding leaf habit, there was no significant difference between deciduous and evergreens for mass-based leafing intensity (Fig. 4b), but volume-based leafing intensity was significantly higher in deciduous than in evergreen species (Fig. 4e).

In the China dataset, one-way ANOVA showed that leaf habit significantly affected volume-based leafing intensity, but leaf habit exerted no significant effect on mass-based leafing intensity (Table 3). There was no significant difference between deciduous and evergreens for mass-based leafing intensity (Fig. 4c). This was

Table 2
Results of two-way ANOVA's for volume- and mass-based leafing intensities for species in the composite dataset.

Factor	df	Mass-based leafing intensity		Volume-based leafing intensity	
		F	P	F	P
Woodiness	1	21.5	<0.001	10.1	0.002
Leaf habit	1	13.7	<0.001	1.0	0.32
Woodiness-leaf habit	1	16.6	<0.001	0.1	0.79

The F-values and P-values are presented for effects of leaf habit, woodiness, and leaf habit-woodiness. Error df is 272 and 394 for volume- and mass-based leafing intensities, respectively.

also the case for the composite dataset. In contrast, volume-based leafing intensity for evergreens was higher than for deciduous (Fig. 4f).

4. Discussion

Our results highlight the likely ecological relevance of leafing intensity beyond its relationship to leaf size variation. The fact that leafing intensity is linked to plant life-history strategies should be mainly attributed to the coordinated relationship of leafing intensity to meristem numbers, because each leaf is normally associated with an axillary meristem in the plant shoot (Rubinstein and Nagao, 1976; Geber, 1990; Bonser and Aarssen, 1996; Whitman and Aarssen, 2010). In this sense, a simple and easily assessed metric (leafing intensity) can be routinely used in screening programs as a proxy for traits that are much more subtle and difficult to assess, e.g. the regenerative potential of a shoot unit. Since plant vegetative growth and reproduction are all derived from meristems, resource allocation decisions in plants are determined by the currency of meristems (Rubinstein and Nagao, 1976; Bonser and Aarssen, 1996; Geber, 1990; Olejniczak, 2001). For a given size of plant shoot, the total number of potentially active meristems available at a given time is finite, and once committed to reproduction, a meristem cannot be redirected to another function (Olejniczak, 2001). Allocation of meristems to current reproduction has the potential for immediate fitness benefits, but it constrains growth (Rubinstein and Nagao, 1976). Conversely, the allocation of meristems to vegetative growth limits current reproductive output, but gains future size and hence (possibly) future reproductive output (Geber, 1990; Cline, 1997; Aarssen, 1995).

Since meristem number is linked with leafing intensity, strategies of resource allocation to vegetative growth versus reproduction can also be judged in terms of plant leafing intensity. In the present study, taller plants have lower leafing intensity (i.e. leaf numbers per shoot size) than smaller plants. This is also reflected in the result that leafing intensity was higher in herbaceous plants than in woody plants (Fig. 4a and d), because herbaceous species are usually shorter than woody species (Ordoñez et al., 2010). Accordingly, these combined results suggest that there is a trade-off between plant apical growth and the size of the axillary meristem (bud) bank per unit plant body size. That is to say, smaller plants with higher leafing intensity (and hence larger axillary bud banks) have greater capacity for flexible meristem deployment (as vegetative or reproductive modules) per unit body size.

At least three hypotheses may be considered for interpreting the higher leafing intensity in smaller species. First, plant height is central to a species' carbon gain strategy, and so competition for light will favor additional expenditure on vertical growth (Falster and Westoby, 2003, 2005), especially involving effects of strong apical dominance (Cline, 1997; Aarssen, 1995). As a result, with fewer large leaves (instead of a large number of small leaves), taller plants benefit more in shading competitors. Second, since small plants cannot win in competition for light, they may compensate for this disadvantage through 'reproductive economy', facilitated by a large bank of meristems, and conferred by high leafing intensity. Thus, small plants have more axillary meristems per unit plant body size that are available for deployment as reproductive units or lateral spread; thus in crowded vegetation associated with shading, and in disturbed habitats where there is limited time availability for reaching reproductive maturity, the high leafing intensity of small plants should maximize the capacity to leave at least some descendants (Aarssen, 2008; Whitman and Aarssen, 2010). Finally, for small plants, a larger meristem/bud bank (and thus a relatively high leafing intensity) may be important in promoting adaptive architectural plasticity, in responding to variation in light

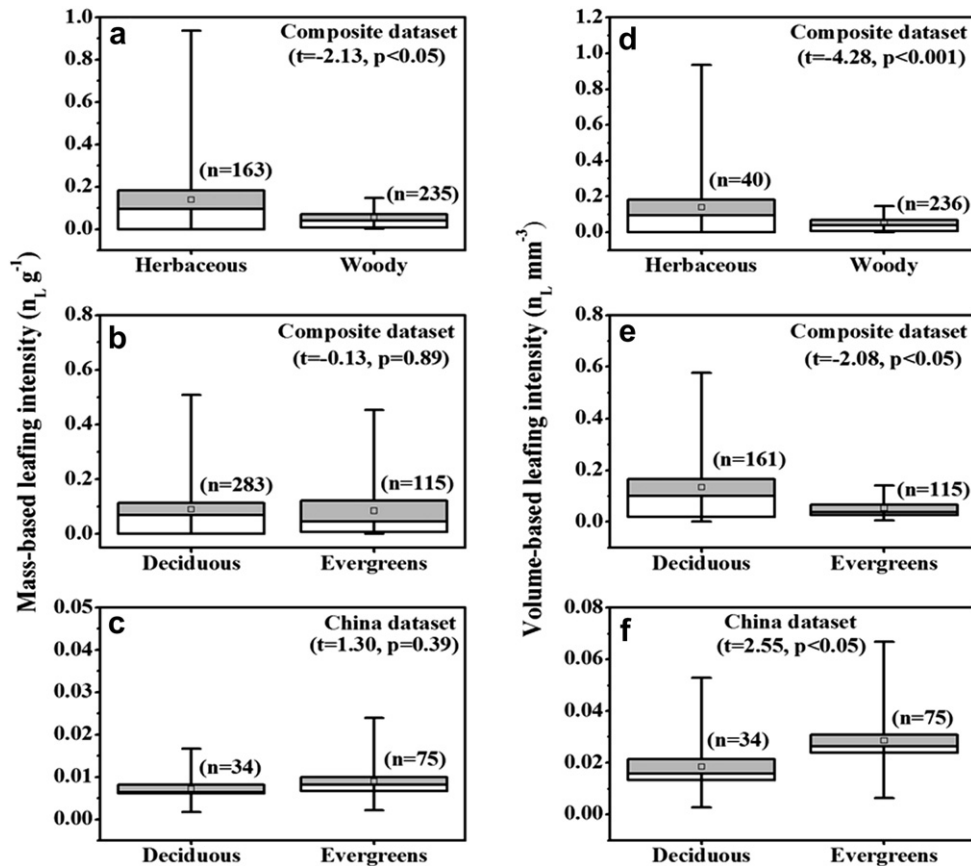


Fig. 4. Differences of leafing intensity for plant species with contrasting leaf habits and growth forms in both the China and the composite datasets. Fig. 4a–c is mass-based leafing intensity; Fig. 4d–f is volume-based leafing intensity. For China dataset, only leaf habit comparison is shown, due to unavailability of data for growth form. Sample sizes are shown with results from Bonferroni test with post hoc testing after two-way ANOVA's for the composite dataset and one-way ANOVA for the China dataset. The square in the middle of the grey box is the mean, the top and bottom boundaries of the grey box represent standard errors, the line dividing the two boxes is the median, and the whisker range indicates the 90% C.I.

availability (Rubinstein and Nagao, 1976; Geber, 1990; Olejniczak, 2001), due to shading stress within multi-species vegetation. In this case, smaller species may adjust optimal shoot and leaf placement for maximizing light interception when the light availability is affected by competition from larger neighboring species. Thus, smaller plants with a relatively large meristem/bud bank may provide greater potential to produce shoots opportunistically, to take advantage of light patches available through the canopy of larger neighboring species (Rubinstein and Nagao, 1976; Geber, 1990; Olejniczak, 2001; Bragg and Westoby, 2002; Kleiman and Aarssen, 2007).

Our results also showed that volume-based leafing intensity was significantly higher in herbaceous and deciduous species than in woody and evergreen species respectively. This phenomenon is certainly consistent with the 'herbivore susceptibility' hypothesis (Mooney et al., 1983; Brown and Lawton, 1991; Coley and Barone, 1996; Haukioja and Koricheva, 2000; Miller et al., 2006; Hanley et al., 2007). Leaf chemistry and certain morphological and

anatomical traits may confer fitness advantages by directly deterring herbivores from feeding (Mooney et al., 1983; Coley and Barone, 1996; Hanley et al., 2007). Plants with hardened leaves and long leaf life span correlate with greater allocation to tannins, phenols or other defensive compounds (Brown and Lawton, 1991; Mole, 1994; Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Haukioja and Koricheva, 2000; Hanley et al., 2007; Ordoñez et al., 2010). Herbaceous and deciduous species have generally less chemical defense than leaves of woody species and evergreen species (Brown and Lawton, 1991; Coley and Barone, 1996; Haukioja and Koricheva, 2000). We speculate that the patterning of leafing intensity between herbaceous and woody species, and between deciduous and evergreen species, might be explained by those general differences in herbivore susceptibilities among growth forms and leaf habits.

The relatively higher leafing intensity in herbaceous and deciduous plants than in woody and evergreen plants may be associated with 'spatial escape' and 'temporal escape' mechanisms. First, herbaceous and deciduous plants with many small leaves (*i.e.* higher leafing intensity) spread out the risk of herbivore attack spatially, thus maximizing the likelihood that at least some leaves are unnoticed (because they are small) and so will remain free from herbivore attack (Brown and Lawton, 1991; Miller et al., 2006; Hanley et al., 2007). This could be particularly important in shorter-lived herbaceous and deciduous species, compared with longer lived woody and evergreen species, since the latter will generally have more future growing seasons within which to recover from leaf tissue loss in any given season (Mole, 1994;

Table 3

Results of one-way ANOVA for volume- and mass-based leafing intensities for species in the China dataset.

Factor	df	Mass-based leafing intensity		Volume-based leafing intensity	
		F	P	F	P
Leaf habit	1	1.7	0.19	6.5	0.01

The F-values and P-values are presented for effects of leaf habit. Error df is 107 for both volume- and mass-based leafing intensities.

Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Haukioja and Koricheva, 2000; Hanley et al., 2007). As a 'temporal escape' mechanism, herbaceous and deciduous plants that produce many leaves (and therefore small ones) may allow leaf presentation more gradually, over a longer time period, thus allowing the plant to compensate later in the growing season ('temporal escape') for leaf tissue loss that occurred earlier in the growing season – instead of producing only a few (large) leaves early in the growing season that might all get damaged (Mooney et al., 1983; Coley and Barone, 1996; Brown and Lawton, 1991; Strauss and Agrawal, 1999; Hanley et al., 2007).

5. Conclusion

The functional relationships of volume-based leafing intensity to plant height, growth form, leaf size, and leaf habit have been described in this study, using a large dataset. We conclude that leafing intensity is a plant trait with relevant functional roles, being ecologically linked with plant resource allocation strategies, particularly with respect to trade-offs between axillary meristem bank size and plant apical growth – and possibly also functionally related to 'spatial escape' and 'temporal escape' mechanisms, arguable on the basis of the 'herbivore susceptibility' hypothesis.

Future studies should explicitly assess the adaptive value of leafing intensity. Here, we have only detected these interesting patterns and speculate about their underlying mechanisms. This is a necessary step to shed light on how to design meaningful tests. Direct tests of the importance of these mechanisms would come from experimental approaches assessing whether or not species with higher leafing intensity recover faster from herbivory, or whether or not plants with higher leafing intensity have greater reproductive capacity or architectural plasticity in shaded understories.

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Appendix 1. Taxonomical groups, leaf habits, arithmetic means of mass-based leafing intensity (LIM, nL g⁻¹) and volume-based leafing intensity (LIV, nL mm⁻³), and plant height for 109 woody plants in the subtropical evergreen broad-leaved forests of eastern China. For the leaf habit, 'd' represented the deciduous broadleaf plants, and 'e' represented the evergreen broadleaf plants.

Family	Species	Leaf habit	LIM (nL g ⁻¹)	LIV (nL mm ⁻³)	Plant height (m)
Aceraceae	<i>Acer olivaceum</i>	d	0.00379	0.01200	2.12
Anacardiaceae	<i>Choerospondias axillaris</i>	d	0.00240	0.00263	19.2
Aquifoliaceae	<i>Ilex latifolia</i>	e	0.00356	0.01860	1.8
Aquifoliaceae	<i>Ilex purpurea</i>	e	0.00543	0.03190	1.98
Aquifoliaceae	<i>Ilex buergeri</i>	e	0.00924	0.02820	3.4
Aquifoliaceae	<i>Ilex kengii</i>	e	0.01075	0.02930	1.07
Betulaceae	<i>Alnus japonica</i>	d	0.00625	0.00730	7.51
Betulaceae	<i>Carpinus viminea</i>	d	0.01660	0.03853	5.97
Caprifoliaceae	<i>Viburnum odoratissimum</i>	e	0.00387	0.01900	3.81
Daphniphyllaceae	<i>Daphniphyllum macropodum</i>	e	0.00466	0.01505	3.71
Ebenaceae	<i>Diospyros glaucifolia</i>	d	0.00610	0.01620	3.73
Ebenaceae	<i>Diospyros kaki</i> var. <i>syvestris</i>	d	0.00322	0.01170	3.82
Elaeocarpaceae	<i>Elaeocarpus japonica</i>	e	0.01008	0.05325	1.47
Elaeocarpaceae	<i>Elaeocarpus glabripetalus</i>	e	0.00587	0.00830	14.92
Ericaceae	<i>Rhododendron ovatum</i>	e	0.02498	0.10550	2.02
Ericaceae	<i>Rhododendron simsii</i>	e	0.04774	0.04960	0.94
Ericaceae	<i>Vaccinium bracteatum</i>	e	0.01234	0.02055	1.55
Ericaceae	<i>Vaccinium mandarinorum</i>	e	0.02202	0.05140	1.29
Ericaceae	<i>Vaccinium trichocladum</i>	e	0.00105	0.00310	11.2
Euphorbiaceae	<i>Mallotus tenuifolius</i>	d	0.00319	0.01630	3.6
Euphorbiaceae	<i>Sapium sebiferum</i>	d	0.02218	0.05274	8.69
Fagaceae	<i>Castanea seguinii</i>	d	0.00656	0.01860	3
Fagaceae	<i>Castanopsis fargesii</i>	e	0.00570	0.02393	10.3
Fagaceae	<i>Cyclobalanopsis stewardiana</i>	e	0.00863	0.04173	8.39
Fagaceae	<i>Castanopsis carlesii</i>	e	0.01779	0.05027	5.16
Fagaceae	<i>Castanopsis sclerophylla</i>	e	0.00536	0.01780	5.65
Fagaceae	<i>Cyclobalanopsis myrsinaefolia</i>	e	0.00864	0.03373	5.75
Fagaceae	<i>Cyclobalanopsis gilva</i>	e	0.00792	0.02347	6.1
Fagaceae	<i>Cyclobalanopsis glauca</i>	e	0.00535	0.01655	5.64
Fagaceae	<i>Cyclobalanopsis gracilis</i>	e	0.00665	0.01380	9.58
Fagaceae	<i>Cyclobalanopsis nubium</i>	e	0.00577	0.02535	17.45
Fagaceae	<i>Lithocarpus glaber</i>	e	0.00770	0.01880	7.94
Fagaceae	<i>Lithocarpus harlandii</i>	e	0.00321	0.01247	11.31
Fagaceae	<i>Quercus fabri</i>	d	0.00369	0.01460	2.6
Fagaceae	<i>Quercus acutissima</i>	d	0.00384	0.00850	3.13
Ginkgoaceae	<i>Ginkgo biloba</i>	d	0.00778	0.01071	11.13
Hamamelidaceae	<i>Distylium myricoides</i>	e	0.00606	0.03010	8.69
Hamamelidaceae	<i>Liquidambar formosana</i>	d	0.00330	0.03030	4.83

Appendix 1. (continued)

Family	Species	Leaf habit	LIM (nL g ⁻¹)	LIV (nL mm ⁻³)	Plant height (m)
Hamamelidaceae	<i>Loropetalum chinense</i>	e	0.02779	0.06480	1.43
Juglandaceae	<i>Pterocarya stenoptera</i>	d	0.00245	0.00277	17.45
Lauraceae	<i>Cinnamomum camphora</i>	e	0.00615	0.02793	11.49
Lauraceae	<i>Cinnamomum japonicum</i>	e	0.00814	0.02290	1.8
Lauraceae	<i>Cinnamomum subavenium</i>	e	0.00395	0.03240	5.4
Lauraceae	<i>Laurus nobilis</i>	e	0.01143	0.02693	6.03
Lauraceae	<i>Lindera reflexa</i>	e	0.00664	0.01907	1.5
Lauraceae	<i>Litsea cubeba</i>	d	0.01257	0.02240	1.1
Lauraceae	<i>Litsea elongata</i>	e	0.00863	0.03620	1.73
Lauraceae	<i>Litsea coreana</i> var. <i>sinensis</i>	e	0.00772	0.01030	1.89
Lauraceae	<i>Machilus leptophylla</i>	e	0.00214	0.01070	10.8
Lauraceae	<i>Machilus thunbergii</i>	e	0.00615	0.02613	2.67
Lauraceae	<i>Neolitsea aurata</i> var. <i>chekiangensis</i>	e	0.00833	0.01725	3.4
Lauraceae	<i>Phoebe sheareri</i>	e	0.00348	0.01830	6.28
Lauraceae	<i>Sassafras tsumu</i>	d	0.00311	0.01240	4.3
Leguminosae	<i>Albizia kalkora</i>	d	0.00452	0.00370	15.32
Leguminosae	<i>Albizia julibrissin</i>	d	0.01428	0.02250	2.01
Leguminosae	<i>Cercis chinensis</i>	d	0.00498	0.01727	1.99
Leguminosae	<i>Dalbergia hupeana</i>	d	0.00254	0.00880	5.11
Leguminosae	<i>Lespedeza chinensis</i>	d	0.00804	0.01010	1.56
Leguminosae	<i>Ormosia henryi</i>	e	0.00103	0.00282	16.4
Magnoliaceae	<i>Illicium lanceolatum</i>	e	0.00598	0.01570	8.43
Magnoliaceae	<i>Magnolia grandiflora</i>	e	0.00088	0.00658	10.37
Magnoliaceae	<i>Michelia maudiae</i>	e	0.00755	0.01260	8.47
Meliaceae	<i>Melia azedarach</i>	d	0.00487	0.04250	4.32
Moraceae	<i>Ficus erecta</i> var. <i>beecheyana</i>	d	0.00543	0.01328	3.25
Myricaceae	<i>Myrica rubra</i>	e	0.00776	0.03583	4.32
Myrtaceae	<i>Syzygium buxifolium</i>	e	0.02248	0.07880	0.96
Nyssaceae	<i>Camptotheca acuminata</i>	d	0.01622	0.08047	3.7
Oleaceae	<i>Ligustrum lucidum</i>	e	0.00861	0.03240	8.9
Oleaceae	<i>Osmanthus cooperi</i>	e	0.00412	0.02415	1.53
Proteaceae	<i>Helicia cochinchinensis</i>	e	0.01152	0.04715	1.57
Punicaceae	<i>Punica granatum</i>	e	0.00719	0.02953	4.44
Rhamnaceae	<i>Hovenia acerba</i>	d	0.00132	0.00285	19.37
Rhamnaceae	<i>Rhamnus crenata</i>	d	0.01017	0.02350	1.2
Rhamnaceae	<i>Rhamnus utilis</i>	d	0.00837	0.01230	2.36
Rosaceae	<i>Photinia serrulata</i>	e	0.01287	0.03390	1.57
Rosaceae	<i>Photinia glabra</i>	e	0.00593	0.03035	2.41
Rosaceae	<i>Raphiolepis indica</i>	e	0.01183	0.03280	1.54
Rubiaceae	<i>Gardenia jasminoides</i>	e	0.01080	0.02794	1.49
Rubiaceae	<i>Lasianthus lancilimbus</i>	e	0.00666	0.02950	1.71
Rubiaceae	<i>Randia cochinchinensis</i>	e	0.00330	0.02160	6.77
Rubiaceae	<i>Tricalysia dubia</i>	e	0.00343	0.00820	2.33
Sabiaceae	<i>Meliosma regida</i>	e	0.00549	0.02260	0.75
Staphyleaceae	<i>Euscaphis japonica</i>	d	0.00177	0.00540	9.98
Styracaceae	<i>Styrax confusus</i>	d	0.00898	0.01830	2.29
Styracaceae	<i>Styrax suberifolia</i>	e	0.00406	0.01250	3.47
Symplocaceae	<i>Symplocos laurina</i>	e	0.00348	0.01040	3.3
Symplocaceae	<i>Symplocos setchuensis</i>	e	0.00528	0.01213	3.42
Symplocaceae	<i>Symplocos sumuntia</i>	e	0.01310	0.04470	1.58
Symplocaceae	<i>Symplocos anomala</i>	e	0.01233	0.03600	1.34
Symplocaceae	<i>Symplocos glauca</i>	e	0.00402	0.00850	2.71
Symplocaceae	<i>Symplocos heishanensis</i>	e	0.01197	0.02440	1.05
Symplocaceae	<i>Symplocos lancifolia</i>	e	0.02397	0.06680	2.54
Symplocaceae	<i>Symplocos paniculata</i>	d	0.00690	0.00930	3.1
Symplocaceae	<i>Symplocos stellaris</i>	e	0.00302	0.00495	8.61
Theaceae	<i>Camellia japonica</i>	e	0.00398	0.02180	1.1
Theaceae	<i>Camellia fraterna</i>	e	0.02317	0.10220	1.86
Theaceae	<i>Camellia oleifera</i>	e	0.00278	0.00910	2.13
Theaceae	<i>Cleyera japonica</i>	e	0.00399	0.01423	1.89
Theaceae	<i>Eurya japonica</i>	e	0.01598	0.05090	1.75
Theaceae	<i>Eurya loquaiana</i>	e	0.01216	0.05040	2.41
Theaceae	<i>Eurya muricata</i>	e	0.00676	0.02030	1.94
Theaceae	<i>Eurya nitida</i>	e	0.01914	0.05950	1.22
Theaceae	<i>Eurya rubiginosa</i> var. <i>attenu</i>	e	0.00883	0.02390	1.66
Theaceae	<i>Schima superba</i>	e	0.00364	0.01802	14.79
Theaceae	<i>Ternstroemia gymnanthera</i>	e	0.00642	0.00630	15.2
Ulmaceae	<i>Aphananthe aspera</i>	d	0.01465	0.01950	2.22
Ulmaceae	<i>Celtis tetrandra</i> ssp. <i>sinensis</i>	d	0.01232	0.04160	4.02
Ulmaceae	<i>Ulmus parvifolia</i>	d	0.00618	0.01380	1.93
Ulmaceae	<i>Zelkova schneideriana</i>	d	0.00613	0.00640	15.66

Appendix 2. Assessment of phylogenetic signal in the evolution of leafing intensity across species

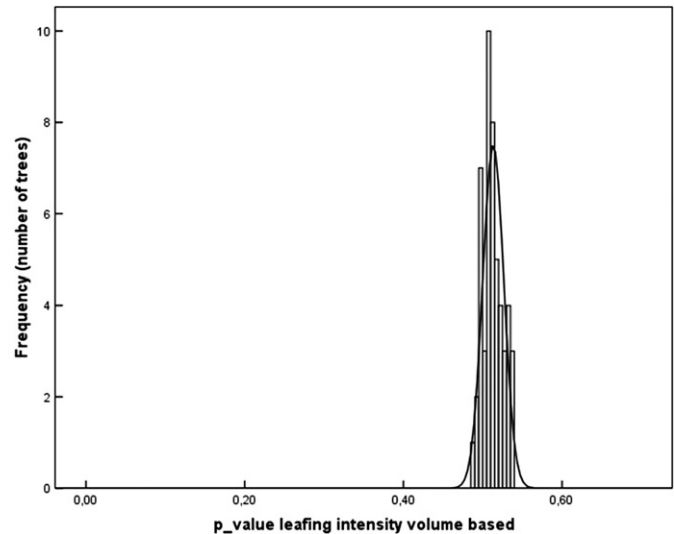
Data on leafing intensity on a volume basis, and on leafing intensity on a mass basis, were log-transformed prior to any analysis to improve normality and homoscedasticity. For carrying out phylogenetic signal analyses on these traits, a phylogeny of the study species was built as follows. Nomenclature and family affiliation of our study genera were checked against the Missouri Botanical Garden's VAST nomenclatural database (W3Tropicos, <http://mobot.mobot.org/W3T/Search/vast.html>). We then built a pruned phylogenetic tree of the seed plants with the study species as terminal tips using the maximally resolved calibrated seed plant tree available in the Phylomatic command of Phylocom 4.1 software (Webb et al., 2006). Note that intra-familial resolution level of Phylomatic 2.0 is remarkably more solved than in previous versions of this tool.

To test for phylogenetic inertia in the evolution of leafing intensity scores, we used the Analysis Of Traits (AOT) module of Phylocom. AOT calculates divergence–convergence degree at each internal node of the tree. Trait means of daughter nodes are computed from the arithmetic mean of the tips of the tree that are linked by ancestry to the daughter node. Then the standard deviation between trait means of daughter nodes is used as a proxy of the degree of divergence at the focal node (i.e. divergence size). High standard deviations between daughter node arithmetic means indicate divergence, whereas the opposite indicates phylogenetic conservatism at that particular bifurcation. Significance of divergence size is estimated by randomly permuting trait values across the tips of the phylogeny. 1000 randomizations were conducted, and the placement of each node-level divergence size score within the distribution of the scores of the 1000 randomizations was used to qualify divergence size at each node as either significant divergence (node-level divergence size at the 5% higher tail of the 20,000 values), significant conservatism (node-level divergence size at the 5% lower tail of the 20,000 values), or non significant change. AOT computes tree-wide conservatism by averaging the node-level scores of divergence size, and tests its statistical significance as explained above.

Phylogenetic uncertainty and the presence of polytomies in the input tree may cause biases in phylogenetically explicit analyses (Butler and King, 2004). Therefore, although AOT procedures are assumed to be robust to the presence of 'soft' polytomies (Webb et al., 2006), we resolved polytomies in the tree by randomly generating 100 fully resolved trees using MESQUITE (Maddison and

Maddison, 2008). We then re-sampled 50 of the 100 fully resolved trees randomly and run the analyses described above again separately for each of those 50 trees.

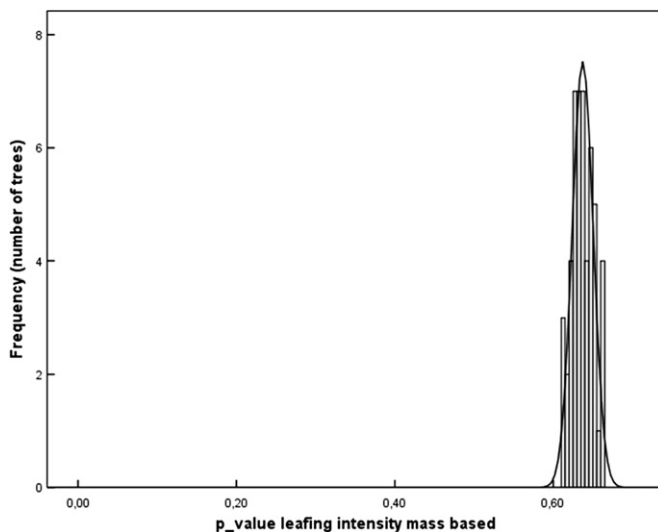
In the graphs below we show the frequency distribution of *P*-values of Phylocom phylogenetic signal tests carried out separately for each of the 50 fully resolved trees.



All *P*-values generated using a set of 50 different trees for each metric were much higher than 0.05, which means that the evolution of leafing intensity does not show phylogenetic signal. This result was robust to phylogenetic uncertainty.

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