

Size-dependent variations in individual traits and trait scaling relationships within a shade-tolerant evergreen tree species

Dong He^{1,2} and En-Rong Yan^{1,2,3}

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¹ Forest Ecosystem Research and Observation Station in Putuo Island, Tiantong National Station for Forest Ecosystem Research, and Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration; School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

² Institute of Eco-Chongming (IEC), Shanghai 200062, China

³ Author for correspondence (e-mail: eryan@des.ecnu.edu.cn)

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PREMISE OF STUDY: The plant size–trait relationship is a fundamental dimension in the spectrum of plant form and function. However, it remains unclear whether the trait scaling relationship within species is modified by tree size. Investigating size-dependent trait covariations within species is crucial for understanding the ontogenetic constraints on the intraspecific economic spectrum and, more broadly, the structure and causes of intraspecific trait variations.

METHODS: We measured eight morphological, stoichiometric, and hydraulic traits for 604 individual plants of a shade-tolerant evergreen tree species, *Litsea elongata*, in a subtropical evergreen forest of eastern China. Individual trait values were regressed against tree basal diameter to evaluate size-dependent trait variations. Standardized major axis regression was employed to examine trait scaling relationships and to test whether there was a common slope and elevation in the trait scaling relationship across size classes.

KEY RESULTS: Small trees tended to have larger, thinner leaves and longer, slenderer stems than larger trees, which indicates an acquisitive economic strategy in juvenile trees. Leaf nitrogen concentrations increased with plant size, which was likely due to a high ratio of structural to photosynthetic nitrogen in the evergreen leaves of large trees. Bivariate trait scaling was minimally modified by tree size, although the elevation of some relationships differed between size classes.

CONCLUSIONS: Our results suggest that there are common economic and biophysical constraints on intraspecific trait covariation, independent of tree size. Small and large trees tend to be located at opposite ends of an intraspecific plant economic spectrum.

KEY WORDS evergreen species; functional trait; intraspecific plant economic spectrum; *Litsea elongata*; plant size; trait scaling.

In nature, the sizes of organisms vary by >21 orders of magnitude (West et al., 1997). In tree species, size variations have important consequences for metabolism, architecture, and functionality (Peters, 1983; Thomas, 1996; Brown et al., 2004). Hence, size variation is one of the major axes of the worldwide spectrum of plant form and function (Díaz et al., 2016). This size-dependent functional dimension in the plant economic spectrum may offer useful insights into the ecological and evolutionary constraints on trait–trait correlation and species' life history trade-offs. Size-dependent trait variations in plants are linked to functional differences, both within and between species. Among these, intraspecific size and trait variations are substantial in plants (Albert et al., 2010; Violle

et al., 2012), especially in tree species, due to their large stature and considerable longevity.

As trees develop, they may experience profound changes in biomechanical burdens, vegetative/reproductive allocation, environmental conditions, and preprogrammed ontogenetic shifts, all of which may induce concomitant changes in tree structure and function (Meinzer et al., 2011; Martin and Thomas, 2013; Damián et al., 2018). Tree size, which is often linked to tree age and/or life stage (Herault et al., 2011), may therefore comprise an important axis of intraspecific trait variability. However, the published spectrum of plant size and function (e.g., Díaz et al. 2016) is often focused on traits measured only at a specific ontogenetic

stage (i.e., adults). Little is known about how tree size variations over multiple ontogenetic stages shape the interspecific variations in individual traits and trait–trait correlations. An exploration of the tree size-dependent functional axis within species may reveal ontogenetic and/or other proximate constraints on trait variation, as opposed to evolutionary constraints on interspecific patterns (Fajardo and Piper, 2011). This knowledge will advance our understanding of the structure and causes of intraspecific trait variations (Albert et al., 2010; Violle et al., 2012; Shipley et al., 2016), which is a critical aspect of functional ecology that has not yet been fully explored.

Much evidence has shown that specific leaf area (the ratio of leaf area to dry mass), leaf nitrogen concentration, and photosynthetic capacity generally decline with increasing plant size (Thomas and Winner, 2002; Hölscher, 2004; Lusk, 2004; Houter and Pons, 2012), whereas wood density exhibits the opposite trend (Githiomi and Kariuki, 2010; Deng et al., 2014; He and Deane, 2016). Experimental evidence in *Helianthus* spp. indicates that photosynthetic rate and leaf nitrogen concentration decrease as plants grow (Mason et al., 2013). Collectively, these findings suggest that plants undergo an ontogenetic shift from resource-acquisitive to resource-conservative strategies (Table 1).

Most studies to date have sampled traits in well-lit habitats, following the standard protocol of Cornelissen et al. (2003). As such, individuals within shaded environments are often excluded; hence, the shifts in functional strategies (e.g., from acquisitive to conservative strategies) for shade-tolerant species remain unquantified. Investigations into the size-dependent intraspecific trait variations of shade-tolerant species will likely provide a renewed understanding of plant functional types and particularly of shade-tolerant syndromes. Shade-tolerant species may possess different ontogenetic patterns of changes in functional strategies, in contrast to light-demanding species (Table 1). For example, ontogenetic changes in photosynthetic and stoichiometric traits may vary between shade-tolerant and -intolerant species due to changes in their reproductive onset times (Thomas, 2010; Martin and Thomas, 2013). Shaded evergreen plants, which typically undergo a slow return on investments of nutrients and dry mass (i.e., conservative strategies), may deploy more nitrogen for structural, rather than photosynthetic, use (Takashima et al., 2004; Lusk and Warton, 2007; Harrison et al., 2009; Sendall and Reich, 2013). Given that shade-tolerant species evolve to have low photosynthetic rates (Reich et al., 1999), and presumably require less photosynthetic

nitrogen, it appears that leaf nitrogen in shade-tolerant species plays as relevant a role in leaf structural rigidity as leaf carbon does in shade-intolerant species. Therefore, we predicted that leaf nitrogen concentrations will increase with tree size in shade-tolerant evergreen species if leaf structural rigidity increases with plant growth (Table 1).

Functional traits do not vary independently, but rather coordinate or trade off with one another (Reich, 2014). As the global leaf economics spectrum has demonstrated, leaf longevity, photosynthetic rate, and leaf nitrogen concentration have universal scaling relationships across plant species at a broad geographic scale (Reich et al., 1997; Wright et al., 2004). These universal scaling relationships suggest that fundamental evolutionary and/or biophysical constraints play critical roles in shaping trait variations among species, and provide a baseline allowing us to identify exceptions due to unique adaptation and acclimation (Reich et al., 1999). Recent studies have revealed that the scaling slopes and/or elevations in interspecific trait relationships differ across plant functional groups and climate regimes (Wright et al., 2005; Bello et al., 2012; Xiang et al., 2013). Considering intraspecific trait variations, it is crucial to explicitly determine whether plant size modifies the apparently universal relationships between key functional traits (e.g., specific leaf area and leaf nitrogen concentration) revealed at the interspecific level (Reich et al., 1997; Wright et al., 2004). Such an endeavor is integral to elucidating the ontogenetic constraints on trait combinations and developing an intraspecific plant economic spectrum.

Compared to small individuals, large trees require higher biomass investments in stems and twigs to provide mechanical support for coping with canopy loading and drag forces that result from wind and rainfall (Niklas and Enquist, 2002). In addition, large trees have to deal with long-distance water transport and deploy leaf and stem structures that are resistant to hydraulic failure (McDowell et al., 2002; Kenzo et al., 2015). As such, there may be varying constraints on individual traits across life stages. Hence, we predicted that trait scaling relationships are altered by tree sizes within species.

We employed a shade-tolerant evergreen tree species, *Litsea elongata*, as a model species to examine size-dependent shifts in individual traits, and trait–trait relationships across eight functional traits. Specifically, we addressed the following questions: (1) How do individual traits vary with plant size? (2) Do trait scaling relationships shift with plant size? Finally, we discuss the implications of size-dependent trait variations for the intraspecific vs. interspecific plant economic spectrum.

TABLE 1. Predicted shifts in individual traits with plant size for shade-tolerant (e.g., *Litsea elongata*) vs. shade-intolerant species. It is well established that plants tend to shift from resource-acquisitive to resource-conservative strategies as they grow. However, where leaf structural rigidity depends on nitrogen concentration, we predicted that larger individuals of shade-tolerant species would have higher leaf nitrogen concentration, opposite to the pattern in shade-intolerant species (see text).

Trait	Acronym	Unit	Conservative/acquisitive indicator with high values	Predicted shift with plant size	
				Shade-intolerant	Shade-tolerant
Leaf area	LA	cm ²	–	↑	↑
Specific leaf area	SLA	cm ² /g	Acquisitive	↓	↓
Leaf dry-matter content	LDMC	g/g	Conservative	↑	↑
Leaf nitrogen concentration	LNC	mg/g	Conservative/acquisitive	↓	↑
Leaf phosphorus concentration	LPC	mg/g	Acquisitive	↑	↑
Specific stem length	SSL	cm/g	Acquisitive	↓	↓
Stem dry-matter content	SDMC	g/g	Conservative	↑	↑
Huber value	HV	cm ² /m ²	Conservative	↑	↑

MATERIALS AND METHODS

Study species and site

Litsea elongata (Nees) J. D. Hooker is an evergreen tree species that prefers shady, moist habitats and occurs commonly in the subtropical evergreen broad-leaved forests across southern China and northern India. Saplings of this species are often abundant in the understory. The maximum diameter at breast height and height of the species are ~40 cm and ~12 m, respectively (Editorial Committee of Flora of China, 1989–2013). Given its relatively low specific leaf area ($150 \pm 0.6 \text{ cm}^2/\text{g}$) and leaf nitrogen concentration ($16.9 \pm 3.3 \text{ mg/g}$), *L. elongata* appears to be a “slow-return” species in the global leaf economics spectrum (see Supplemental Data with this article, Appendix S1).

We measured functional traits and tree sizes of the target species in the Tiantong National Forest Park (29°41′–50′N, 121°36′–52′E) of Zhejiang province in eastern China. This area has a subtropical monsoon climate, with a mean annual temperature of ~16.2°C and mean annual precipitation of ~1375 mm (Song and Wang, 1995). The park comprises ~349 ha and preserves a wealth of natural habitats and vegetation. The zonal vegetation is represented by evergreen broad-leaved forests.

In the interior of the Tiantong National Forest Park, we selected a 1 ha plot, with little human disturbance over the past 30 yr, for the present study. The slope of the plot was about $30 \pm 6^\circ$, and the elevation ranged between 330 and 400 m. The soil volumetric water content within the 1 ha plot was $33.4 \pm 1.6\%$, and total nitrogen concentration was $3.5 \pm 0.6 \text{ mg/g}$ (E.-R. Yan, unpublished data). The dominant community composition is characterized by the genera *Castanopsis* (Fagaceae), *Cyclobalanopsis* (Fagaceae), *Machilus* (Lauraceae), and *Litsea* (Lauraceae) in the upper-story stratum, and *Camellia* (Theaceae), *Eurya* (Theaceae), and *Symplocos* (Symplocaceae) in the understory stratum.

Plant and trait sampling

We limited our sampling to deep understory shade, following the approach of Poorter (2007). Specifically, we sampled plants only under closed forest canopies with exposure to as little lateral light as possible. Large trees (>9 m tall) that were fully exposed to sunlight, or that received ample overtop light, were excluded from our sampling because our main focus was on shade-tolerant individuals. In total, 604 individual trees were selected for measures of basal diameter, tree height, and functional traits (GB/T 33027-2016: “Observation Methodology for Long-term Forest Ecosystem Research” of National Standards of the People’s Republic of China, <http://www.sac.gov.cn/>). The upper limits of the sampled tree size were 14.5 cm in basal diameter and 9 m in height. It should be noted that this size range allowed us to cover several life stages, albeit not the full life cycle of the target species.

For each tree, we cut two or three current-year twigs from the outer canopy. Branches above 1.8 m were accessed with the help of a tree pruner. We were careful to select the twigs with fully developed and healthy-looking leaves. All leaves were detached from the twigs to determine their individual leaf area, as well as their fresh and dry weights (Pérez-Harguindeguy et al., 2013). Each twig contained three to fifteen leaves, with an average of five leaves. We then proceeded to measure the following three leaf traits: individual leaf area (with a LI-3000C leaf area meter), specific leaf area, and leaf

dry-matter content (the ratio of dry to fresh weight). Based on the dried twig-specific leaf samples, we determined leaf nitrogen and phosphorus concentrations per unit mass using a flow-injection auto analyzer (SAN++; Skalar, Breda, The Netherlands).

After removal of leaves, we measured twig dimensions (diameter at the two ends and the middle point, as well as overall twig length) with a vernier caliper. On average, the twigs were $0.2 \pm 0.1 \text{ cm}$ in diameter and $5.9 \pm 5.2 \text{ cm}$ in length. The fresh mass was subsequently determined for twigs, and dry mass was measured following a 72 h oven treatment at 120°C. The stem dry-matter content was defined as the ratio of the dry twig to fresh mass. Specific stem length was defined as the ratio of twig length to dry mass, indicating the capacity of axial growth and elongation for a given stem biomass (Poorter and Rose, 2005). Finally, we approximated the Huber value, a proxy for the hydraulic capacity of branches or whole plants, by dividing the mean cross-sectional area of a given twig by the total attached leaf area (Huber, 1928). For each trait, trait values were averaged for individual trees.

Statistical analyses

We tested the pairwise correlation between eight traits using standardized major axis (SMA) regression. Because of the large number of correlations ($C_8^2 = 28$), the *P* value for rejecting noncorrelation was adjusted to 0.004 following the Bonferroni method. To investigate multivariate trait relationships, we performed principal component analysis (PCA) over all eight traits. Subsequently, we regressed individual traits against plant size (i.e., basal diameter). The values of all traits, except for leaf and stem dry-matter content, were left-skewed and log transformation was carried out prior to regression.

To examine whether trait relationships shifted with tree size, we divided the 604 individuals into two size classes: (1) large and (2) small. Individuals with both basal diameter >4 cm and height >3.5 m were defined as the large class, whereas the remaining were grouped as the small class. Because the size distribution was left-skewed, a wide range was set for the large size class. The large and small classes included 382 and 222 individuals, respectively. To evaluate possible bias associated with the defined size classes (i.e., diameter: 4.3 cm, height: 3.5 m), we followed an alternative procedure for size classification. In this procedure, small and large classes were grouped by selecting 100 individuals around the 25th and 75th percentile values of the basal diameter of trees, respectively. Here, the size difference was enlarged between two classes.

We employed SMA regression to examine the size-class-specific bivariate relationships between traits. Bivariate relationships that passed the previous correlation tests were scrutinized further. We tested whether there was a common slope in SMA lines between size classes. If the common slope was justified, we conducted further tests on elevation shifts between size classes. These tests were repeated for the alternative size classification scenarios.

All statistical analyses were conducted in R (R Core Team, 2017), with the aid of the R package “smatr” (Warton et al., 2012) for dealing with SMA regressions and tests.

RESULTS

Across all surveyed trees, basal diameter varied 29-fold (Table 2). The most variable traits were specific stem length, Huber value, and

TABLE 2. Mean values and ranges of functional trait values in *Litsea elongata*.

Trait	Mean	CV	Minimum	Maximum	Global reference range
BD (cm)	3.87	56.70%	0.50	14.50	0.1–40
LA (cm ²)	19.12	34.00%	3.18	48.32	1–6.4*10 ⁵
SLA (cm ² /g)	149.86	17.40%	89.08	269.61	10–3000
LDMC (g/g)	0.43	11.40%	0.28	0.74	0.05–0.70
LNC (mg/g)	16.94	19.60%	5.78	42.05	5–70
LPC (mg/g)	0.44	47.90%	0.10	1.46	0.2–5
SSL (cm/g)	94.62	40.35%	17.85	350.00	Unknown
SDMC (g/g)	0.38	19.90%	0.15	0.85	0.15–0.85
HV (cm ² /m ²)	2.54	52.90%	0.85	19.17	0.1–100

Notes: BD = basal diameter; for trait acronyms, see Table 1. Data sources for global reference range: Editorial Committee of Flora of China (1989–2013), Martínez-Vilalta (2011), and Pérez-Harguindeguy et al. (2013).

leaf phosphorus concentration. These traits varied >15-fold, with the coefficients of variation >40%. By contrast, specific leaf area, leaf dry-matter content, leaf nitrogen concentration, and stem dry-matter content varied <8-fold, with coefficients of variation <20%. Leaf area was moderately varied (CV = 34 %).

The strength of all pairwise correlations between eight traits was fairly low ($R^2 \leq 0.42$; Table 3). Among the significant relationships, the weakest correlations were found between leaf area and specific leaf area, and between leaf nitrogen concentration and specific leaf area ($R^2 = 0.02$ in both instances). The strongest correlation was that between leaf area and Huber value ($R^2 = 0.42$). Leaf area scaled negatively with specific leaf area, specific stem length, and Huber value. Specific leaf area was positively correlated with specific stem length, which meant that larger and/or thinner leaves were more common on longer and slenderer stems. Specific leaf area was also positively related to leaf nitrogen concentration, but negatively related to dry-matter content in both leaves and twigs. Leaf nitrogen and phosphorus concentrations, as well as leaf and stem dry-matter content, were positively associated (Table 3 and Appendix S1). Specific stem length was negatively related to stem dry-matter content, but positively related to Huber value.

PCA revealed that the first axis accounted for 29% of total variation across eight traits, where high specific leaf area and specific stem length characterized one end, and high dry-matter content (i.e., leaf and stem dry-matter content) characterized the other end (Fig. 1). The second axis captured 21% of the total variation, which was primarily defined by the negative relationship between leaf area and Huber value, and to a lesser extent by leaf nitrogen and phosphorus concentrations.

On average, leaf area and leaf nitrogen concentration increased with increasing plant size (Fig. 2A, D). By contrast, specific leaf area and specific stem length decreased with increasing plant size

(Fig. 2B, F). Leaf dry-matter content, leaf phosphorus concentration, stem dry-matter content, and Huber value did not show any directional shift with increasing plant size (Fig. 2C, E, G, H). Large individuals were more inclined toward the lower end of the first axis of PCA (i.e., higher leaf and stem dry-matter content), while small individuals showed the opposite trend (Fig. 1B).

Leaving aside the noncorrelated trait pairs, nearly all bivariate trait relationships showed invariant scaling exponents (i.e., slopes) between two size classes (Table 4 and Fig. 3). One exception was that the slope of the relationship between stem dry-matter content and specific leaf area varied between size classes (Table 4 and Fig. 3D). There was a greater reduction in stem dry-matter content with per unit increase in specific leaf area in the small than in the large class (Table 4). Additionally, the significant relationship between leaf nitrogen concentration and specific leaf area was found only in large individuals (Table 3 and Fig. 3B).

With respect to those invariant trait scaling relationships between size classes, significant intercept shifts were found for the relationships between trait-pairs of specific leaf area and leaf dry-matter content (Fig. 3A), specific stem length and leaf dry-matter content (Fig. 3E), and specific stem length and stem dry-matter content (Fig. 3F). This indicated that, for a given value of specific leaf area or specific stem length, the dry-matter contents of leaves and stems were greater in the small class than in the large class (Table 3 and Fig. 3). By contrast, the intercept did not shift in the relationship between specific leaf area and specific stem length over tree size classes (Fig. 3B). The alternate size classification scheme (i.e., based on the 25th and 75th percentiles) did not alter the shifting patterns of slopes and intercepts in the bivariate trait relationships described above (Appendix S2). This result confirmed that the definition of our two tree size classes (small and large), based on a cut-off value of 4.3 cm for diameter and 3.5 m for height, was unbiased.

TABLE 3. Pairwise relationships between functional traits for *Litsea elongata* as revealed by standardized major axis regression.

	LA	SLA	LDMC	LNC	LPC	SSL	SDMC	HV
LA		-0.46	-0.32	0.53	1.34	-0.88	0.77	-1.04
SLA	0.02		-0.62	0.95	2.93	1.95	-0.91	-2.30
LDMC	<0.01	0.36		-1.69	-4.30	-0.32	1.50	3.35
LNC	<0.01	0.02	<0.01		3.11	-1.83	1.35	-2.05
LPC	<0.01	<0.01	<0.01	0.10		-0.71	0.52	-0.80
SSL	0.36	0.25	0.09	<0.01	<0.01		-0.49	1.17
SDMC	<0.01	0.07	0.13	<0.01	<0.01	0.18		1.40
HV	0.42	<0.01	0.01	<0.01	<0.01	0.08	<0.01	

Notes: For trait acronyms, see Table 1. Slope exponents are shown above the diagonal, with bold values indicating significant relationships; Bonferroni adjustment ($P < 0.004$) was implemented for rejecting noncorrelation. Coefficients of determination (R^2) are shown under the diagonal.

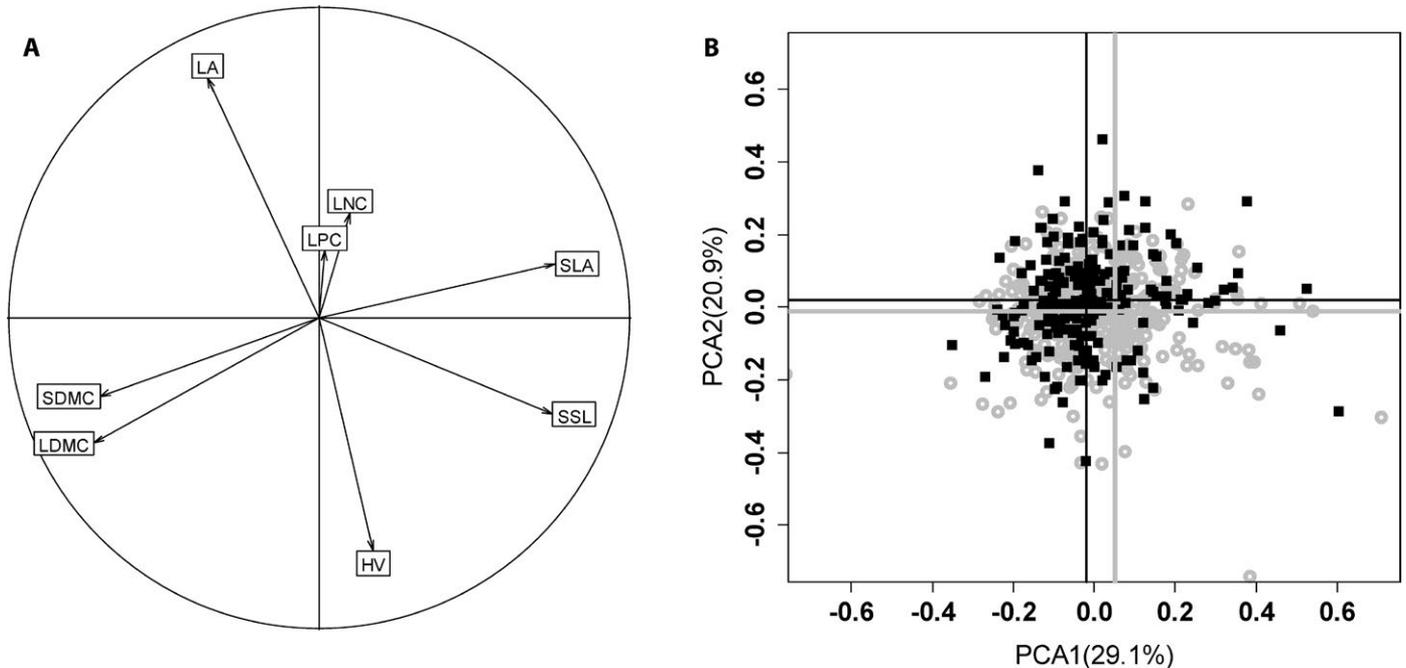


FIGURE 1. Principal component analysis (PCA) of eight functional traits in *Litsea elongata*: (A) biplot of the first two principal components loaded by trait variables; and (B) distribution of the two size classes along the first two axes. The small and large size classes are represented by gray and black, respectively. The crossings show the mean positions of the two size classes. The proportions of total variation explained by the first and second principal components are in parentheses next to axis labels.

DISCUSSION

How do individual traits vary with tree size?

We found that specific leaf area declined significantly with plant size in *L. elongata*, which was in agreement with the widely observed pattern in several other plant species with different life-forms and habitats (Hölscher, 2004; Ishida et al., 2005; Martin and Thomas, 2013). Given the increased leaf area in large plants, the observed decline in specific leaf area may be associated with an optimization strategy in resource allocation (Prentice et al., 2014). Large-area leaves typically require additional structural support (Milla and Reich, 2007; Niinemets et al., 2007); however, young or small plants are too resource-limited to afford high construction costs and slow revenue per area. In addition, preprogrammed ontogenetic shifts might also contribute to the decline in specific leaf area (Apple et al., 2002; Thomas and Winner, 2002). Strong hydraulic constraints in large and presumably tall plants are supposed to favor a low specific leaf area, in that a low specific leaf area may promote tolerance to cell collapse that is induced by low water potential at high canopy positions (Niinemets, 2002; Thomas and Winner, 2002; Kenzo et al., 2015). However, this mechanism may not be important in *L. elongata*, at least within the surveyed size range, given that we did not observe a significant increase in Huber value with increasing plant size.

As a functional analogue of specific leaf area for stems, specific stem length also decreased with plant size. This shift might again be attributed to an optimization strategy in resource allocation; to acquire diffusive light more efficiently, small-leaved saplings tended to have long and slender twigs with a given amount of biomass. Along with the high specific leaf area in small individuals, the functions of

twigs and leaves were coordinated. In this regard, *L. elongata* exhibited some characteristics of a “fast-return” economy (*sensu* Reich, 2014) at the early life stage. With low specific leaf area and specific stem length for large individuals, the results gave some credence to the proposition that plant size increased at the expense of metabolic and energetic decline (Niklas and Cobb, 2008).

As predicted, leaf nitrogen concentration was, on average, higher in larger individuals. This seemed to be in conflict with the “slow-return” nutrient economy that has been widely observed at the late life stage of plants. There is ample evidence for the decline of mass-based photosynthetic rate during plant growth (Thomas and Winner, 2002; Ishida et al., 2005). In agreement with the photosynthetic decline, Houter and Pons (2012) observed a decrease in leaf nitrogen concentration in adult trees. However, the pattern of leaf nitrogen varying with plant size may be different in shade-tolerant evergreen species (Sendall and Reich, 2013). In shade-tolerant evergreen species, a considerable fraction of structural nitrogen is found to be associated with tissue construction (Takashima et al., 2004; Harrison et al., 2009). This contrasts with the commonly held notion that higher leaf nitrogen promotes photosynthesis (Reich et al., 1999).

Higher leaf nitrogen concentrations in larger *L. elongata* individuals might be due to elevated nitrogen investments in leaf structural rigidity (i.e., low specific leaf area) rather than in photosynthetic biochemistry. Further investigation is required to confirm this hypothesized causality. This might be achieved experimentally by decomposing the leaf nitrogen concentration into structural vs. photosynthetic components in *L. elongata*, and/or testing a wider array of shade-tolerant evergreens. Regardless of which strategy is employed, how a functional trait varies its functional role in disparate taxa and habitats is a vital clue toward understanding the exceptions to trait relationships.

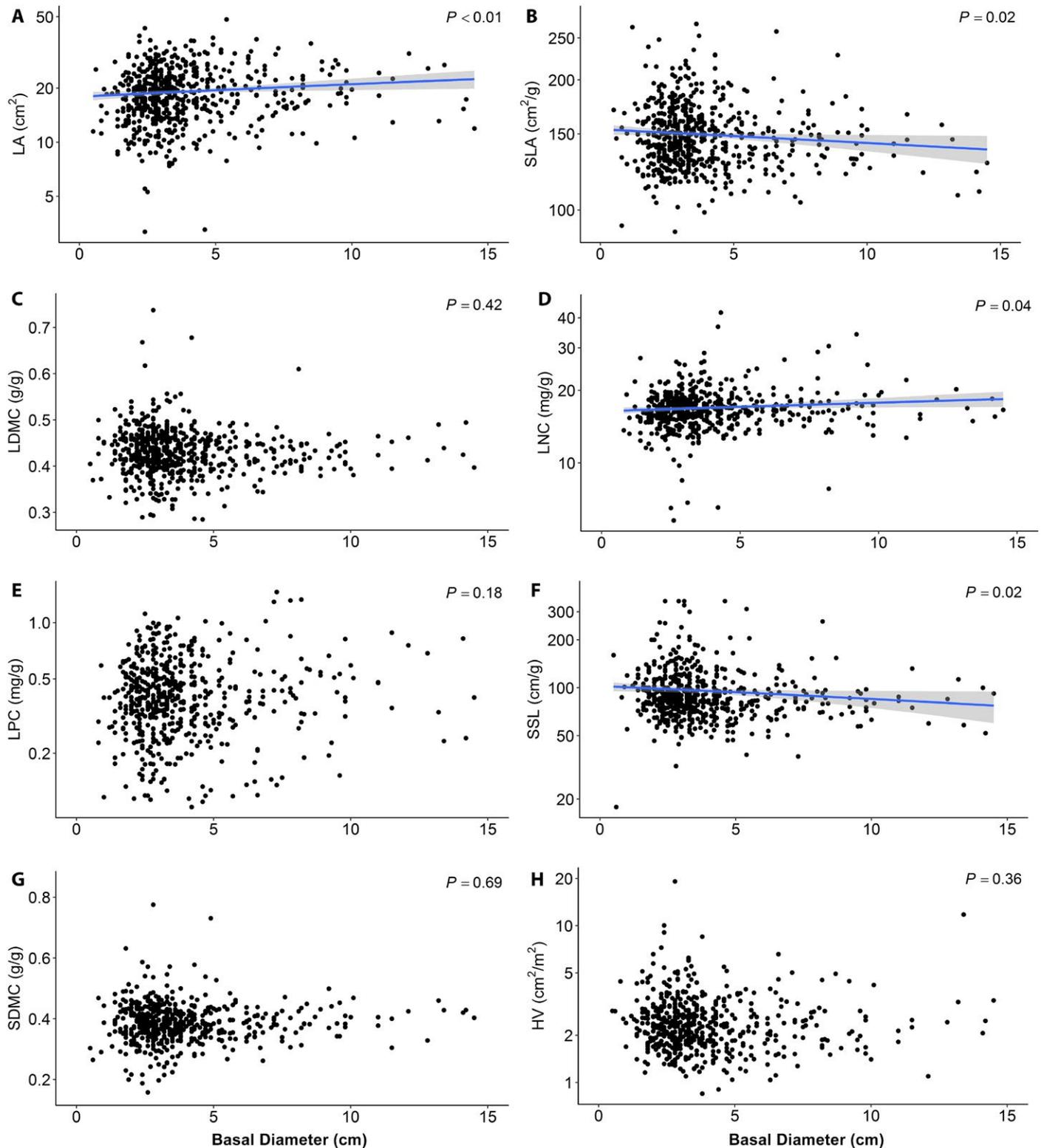


FIGURE 2. Individual functional traits in relation to tree size (i.e. basal diameter) as revealed by linear models. The significance (P) of each test is shown at the panel corner. Blue lines indicate significant relationships; gray bands around blue lines represent 95% confidence intervals of regression lines. Note that most traits as response variables are shown on a natural log scale, except LDMC and SDMC. Acronyms: SLA = specific leaf area, LA = leaf area, LDMC = leaf dry-matter content, LNC = mass-based leaf nitrogen content, LPC = mass-based leaf phosphorus content, SDMC = stem dry-matter content, SSL = specific stem length, HV = Huber value.

TABLE 4. Bivariate trait relationships in two size classes for *Litsea elongata*.

	Small class			Large class			Common slope test	Common elevation test
	α	β	R^2	α	β	R^2		
ln(SLA) vs. ln(LA)	6.31	-0.45	0.02	6.30	-0.46	0.02	$P = 0.97$	$P = 0.89$
ln(SSL) vs. ln(LA)	7.10	-0.90	0.37	6.94	-0.85	0.34	$P = 0.45$	$P = 0.94$
ln(HV) vs. ln(LA)	3.83	-1.06	0.45	3.84	-1.00	0.37	$P = 0.40$	$P = 0.95$
ln(LDMC) vs. ln(SLA)	2.42	-0.65	0.37	2.04	-0.58	0.58	$P = 0.13$	$P < 0.01$
ln(LNC) vs. ln(SLA)	-2.05	0.97	0.01	-1.99	0.97	0.05	–	–
ln(SSL) vs. ln(SLA)	-5.53	2.01	0.24	-4.85	1.87	0.26	$P = 0.41$	$P = 0.85$
ln(SDMC) vs. ln(SLA)	3.96	-0.98	0.07	3.06	-0.81	0.08	$P = 0.03$	–
ln(SDMC) vs. ln(LDMC)	0.31	1.51	0.13	0.30	1.46	0.14	$P = 0.64$	$P = 0.66$
ln(LPC) vs. ln(LNC)	-9.34	3.34	0.12	-9.72	3.30	0.08	$P = 0.31$	$P = 0.11$
ln(LDMC) vs. ln(SSL)	0.62	-0.34	0.09	0.59	-0.31	0.11	$P = 0.32$	$P < 0.01$
ln(SDMC) vs. ln(SSL)	1.36	-0.52	0.20	1.07	-0.46	0.15	$P = 0.23$	$P = 0.02$
ln(HV) vs. ln(SSL)	-4.32	1.15	0.10	-4.62	1.22	0.03	$P = 0.55$	$P = 0.84$

Notes: For trait acronyms, see Table 1. α and β are elevation and slope of standardized major axis (SMA) regression, respectively. R^2 is the coefficient of determination in SMA regression, with bold numbers indicating significant relationships. Common slope tests examined whether SMA lines of different size classes shared a common slope; and, with a common slope justified, common elevation tests examined whether different size classes had no elevation shift.

Large trees have to manage water transport over long distances, which promotes increased hydraulic resistance (Kenzo et al., 2015). We suspected that this would favor high stem dry-matter content that is resistant to transport failure rather than hydraulically efficient. For the same reason, large trees would show a high Huber value, with less transpiring area per cross-sectional conductive area (McDowell et al., 2002). However, we did not detect any shifts in stem dry-matter content or Huber value with plant size. Because the hydraulic path length is largely a function of plant height rather than of diameter, we also examined the relationships of stem dry-matter content and log Huber value with plant height. Neither of the two traits showed any height-related shifts ($P = 0.95$ for stem dry-matter content; $P = 0.07$ for log Huber value). A possible explanation is that water did not act as a severe limiting factor for *L. elongata* in the present study, because of ample rainfall in a monsoon climate and resulting high soil moisture.

How do trait scaling relationships shift with tree size?

The direction of bivariate trait relationships in *L. elongata* was broadly consistent with expectations under functional convergence along the worldwide “fast–slow” plant economic spectrum (Reich, 2014). For instance, there were significant positive relationships between specific leaf area and leaf nitrogen concentration, between specific leaf area and specific stem length, and between leaf dry-matter content and stem dry-matter content, whereas negative relationships were found between specific leaf area and leaf dry-matter content, and between specific stem length and stem dry-matter content (Table 2 and Appendix S1). Similar to the results obtained in the tropical crop species *Coffea arabica* (Martin et al., 2017), the strength of the bivariate trait relationships within species in this study was also quite low, compared with those of cross-species patterns.

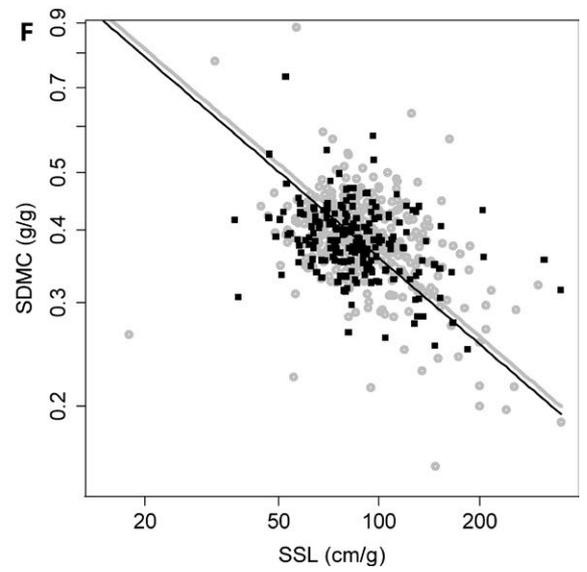
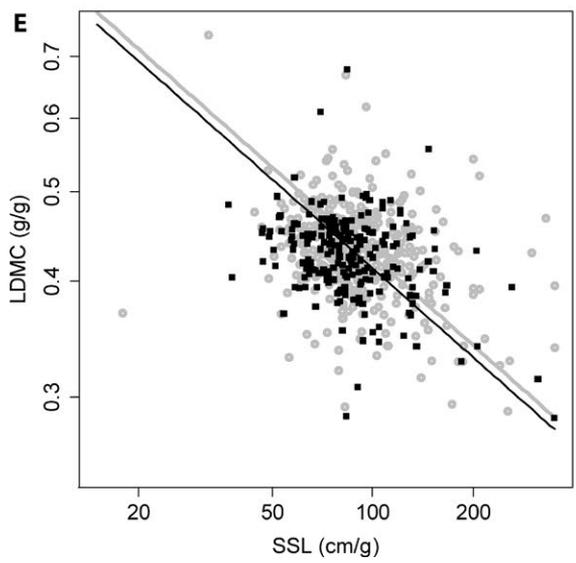
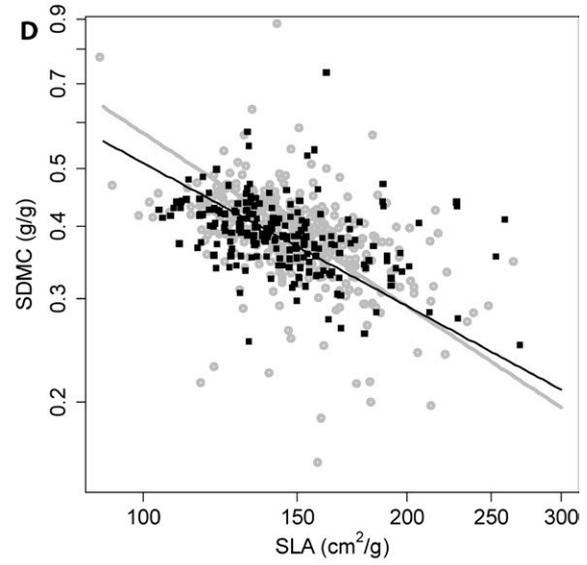
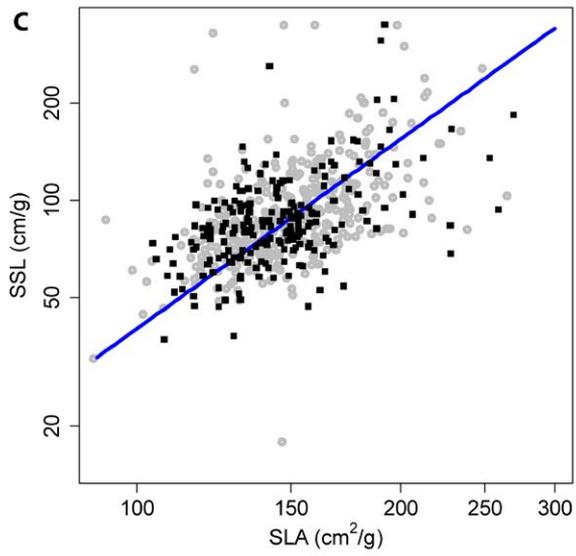
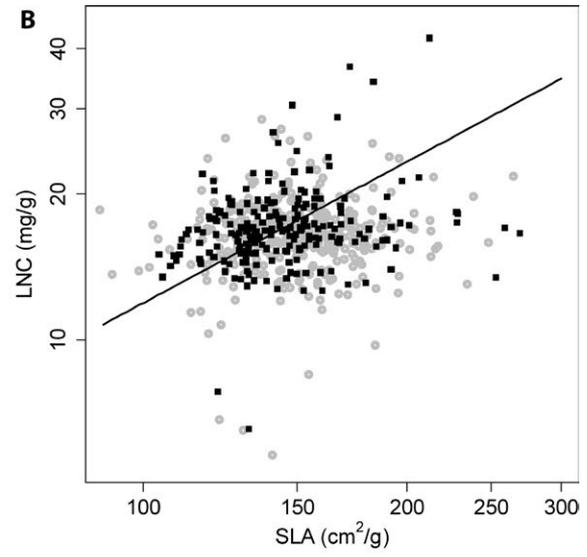
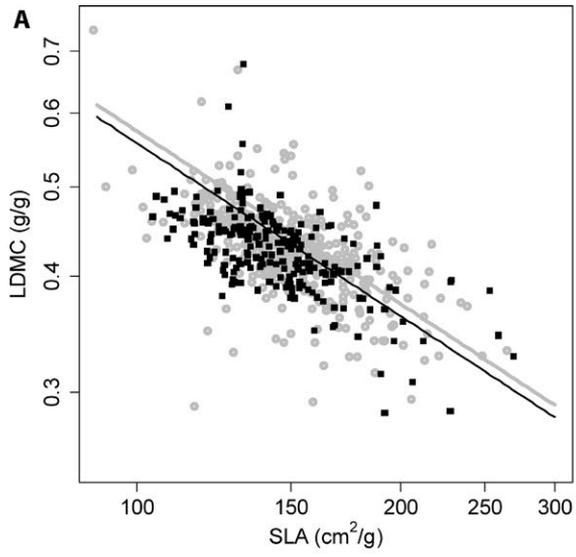
In contrast to expectation, specific leaf area and leaf nitrogen concentration in the small class of *L. elongata* were poorly related.

They were also uncorrelated in the shade-tolerant evergreen species *Quercus ilex* (Niinemets, 2015). This pattern deviated radically from the close coupling between the two traits in the global leaf economics spectrum (Wright et al., 2004; Díaz et al., 2016). The underlying reason was probably associated with high structural nitrogen concentrations in evergreen leaves. Moreover, plant size appeared to have a role in undermining their otherwise strong relationship, in that specific leaf area and leaf nitrogen concentrations varied with plant size in opposite ways.

We found that bivariate trait relationships were largely invariant between plant size classes. The log–log scaling exponents of most trait relationships did not differ among size classes, except for the relationship between stem dry-matter content and specific leaf area. For instance, a twofold increase in specific leaf area was always accompanied by a 0.7-fold ($e^{-0.62 \ln 2}$) decrease in leaf dry-matter content, and by a 3.9-fold ($e^{1.95 \ln 2}$) increase in specific stem length, regardless of plant size class. These results contrast with our hypothesis that trait relationships could be altered by plant size due to varying resource availability and hydraulic constraints on individual traits across life stages. Instead, our results support an alternate proposition that common constraints existed on intraspecific trait covariation, being largely independent of life stages. Because our study was restricted to a local area, we surmised that the common constraints stemmed from economic optimization and fundamental biophysical rules. Here, the role of evolutionary selection in regulating the interspecific trait scaling at geographic scales (Reich et al., 1997, 1999) might be less important.

Although the slope exponents in the trait scaling relationships were found to be invariant in *L. elongata*, there were size-class-specific elevations in the bivariate relationships between specific leaf area and leaf dry-matter content, between specific stem length and leaf dry-matter content, and between specific stem length and stem dry-matter content. For given values of specific leaf area or specific stem, the leaf and stem dry-matter content were higher in smaller than in larger individuals, which suggested that larger

FIGURE 3. Trait scaling relationships for the small (gray circles) and large (black squares) size classes as revealed by standardized major axis (SMA) regressions (for coefficients of SMA, see Table 4). No line is shown if the bivariate trait relationship for a size class is not significant. A single blue line shows a common slope with common elevation between two size classes. Two parallel lines show a common slope but with unequal elevation, and two crossover lines show heterogeneous slopes. Because trait scaling relationships are examined on a log–log basis, all trait values are shown on a natural log scale.



trees required more water to achieve the same growth potential as smaller trees. In other words, with an identical supply of water and dry mass, there may be a greater potential for growth in the early life stages. Along with the observation of greater reduction in stem dry-matter content per unit increase in the specific leaf area of small individuals (i.e., more negative slope in the relationship of stem dry-matter content and specific leaf area), these results again support the idea that smaller plants tend to adopt more acquisitive strategies than larger plants (Mason et al., 2013).

Closing remarks

In an attempt to establish an intraspecific leaf economics spectrum, Niinemets (2015) argued that plant size may potentially influence the scaling relationships between traits. The present study has identified a major axis that is positively loaded by specific leaf area and specific stem length (i.e., the fast-return end), and negatively loaded by leaf dry-matter content and stem dry-matter content (i.e., the slow-return end) within a shade-tolerant species, *Litsea elongata*. We found that size-dependent variations in individual traits were trait-specific; however, the slopes of trait scaling relationships were virtually constant across size classes. Our results highlight the prominent role of common economic and biophysical constraints in regulating intraspecific trait covariation as being largely independent of tree size. Given that small and large individuals exhibited contrasting characteristics of fast- and slow-return economy, respectively, we argue that intraspecific trait syndromes have profound implications for understanding the size-dependent phenotypic integration of resource capture and investment.

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AUTHOR CONTRIBUTIONS

E.-R.Y. collected the data and D.H. analyzed the data. Both authors conceived the ideas and prepared the manuscript.

DATA ACCESSIBILITY

Please see Appendix S3 for raw data of plant size and functional trait values.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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