



Research paper

Strong intraspecific trait variation in a tropical dominant tree species along an elevational gradient

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ABSTRACT

Functional trait variation of plant species includes both inter- and intraspecific variation; however, trait-based plant ecology generally considers only interspecific variation while ignoring intraspecific variation. One reason for this neglect is that intraspecific variation may be negligible when compared to interspecific variation; however, direct comparisons between inter- and intraspecific variation of plant species are lacking, especially in tropical forests. Here we investigated intraspecific leaf trait variation (leaf area, specific leaf area, leaf thickness, leaf density, leaf chlorophyll content) of *Pittosporopsis kerrii* Craib (Icacinaeae), the most abundant tree species in the Xishuangbanna tropical seasonal rainforest in southwestern China, along an elevational gradient (703–824 m). We found a substantial range of intraspecific variation in *P. kerrii* that was never less than 22.1% of range of the interspecific variation among 462 tree species reported before in the same community. Moreover, with increased elevation, both leaf thickness and density increased and specific leaf area decreased significantly. It could be more important for the individuals of *P. kerrii* to produce thicker and denser leaves to tolerate environmental stress (e.g. soil water availability) rather than having high growth rates at the places with higher elevation in the Xishuangbanna tropical seasonal rainforest.

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1. Introduction

Trait-based plant ecology, which focuses on plant functional traits rather than taxonomic identities, has been shown to be a feasible approach to explore a wide range of research problems in ecology (Wright et al., 2004; McGill et al., 2006; Kunstler et al., 2016). Functional traits, by definition, are any measurable feature at the individual level affecting fitness directly or indirectly (Violle et al., 2007; Albert et al., 2010, 2012). Therefore, functional trait variation of plants within a community consists of both inter- and intraspecific variation, i.e., variation of averaged trait value between species and trait variation of individuals within species, respectively. Ecologists have long used mean trait values of species to infer

ecological processes (McGill et al., 2006). However, recent studies have shown that intraspecific variation is substantial and plays an important role in community assembly and ecosystem processes (Siefert et al., 2015; Hart et al., 2016; Turcotte and Levine, 2016; Pérez-Izquierdo et al., 2019).

Intraspecific variation in plants may help species adapt to diverse abiotic and biotic environments (Jung et al., 2010; Violle et al., 2012; Silva et al., 2019), affect species coexistence (Crutsinger et al., 2008; Clark, 2010; Turcotte and Levine, 2016), and alter ecosystem processes (Schweitzer et al., 2004; Crutsinger et al., 2006). For example, in Brazil, intraspecific variation in *Eremanthus erythropappus* promotes its ability to occupy different habitats (forests and savannas) (Silva et al., 2019). Similarly, intraspecific variation of seed biomass in *Brachypodium hybridum*, an annual grass in California, facilitates its invasions into water-limited environments (Liu et al., 2019). Intraspecific variation has also been shown to impact species coexistence, with stable coexistence predicted when stabilizing niche differences exceed average fitness differences, and competitive exclusion predicted when it does not

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(Turcotte and Levine, 2016). The importance of intraspecific variation to competitive exclusion has been demonstrated in *Solidago altissima*, a plant which reduces richness, cover, and biomass of new colonizing species within communities by increasing stem density (Crutsinger et al., 2008). Intraspecific variation can also affect various ecosystem processes, the condensed tannins in the leaves of cottonwood trees of different genotypes in both *Populus fremontii* and *P. angustifolia* have been found to significantly affect litter decomposition and soil N mineralization (Schweitzer et al., 2004). In *Pinus pinaster*, intraspecific variation has been shown to affect its rhizospheric microbiome and the hydrolysis of celluloses, hemicelluloses, and chitin (Pérez-Izquierdo et al., 2019).

Although many studies have shown that plant traits vary substantially within species, and recent syntheses have encouraged the inclusion of intraspecific trait variation into ecological studies (Hulshof and Swenson, 2010; Bolnick et al., 2011; Violle et al., 2012; Siefert et al., 2015; Yang et al., 2018), direct comparisons between inter- and intraspecific variation of tropical plant species are still lacking. One key factor that is generally agreed to affect plant intraspecific variation is elevation (Cordell et al., 1998; Fajardo and Piper, 2011; Read et al., 2014). Therefore, in this study we compared the intraspecific leaf trait variation (leaf area, specific leaf area, leaf thickness, leaf density, and leaf chlorophyll content) of *Pittosporopsis kerrii* Craib (Icacinaeae) along an elevation gradient with that

Table 1
A direct comparison of leaf functional traits between the intraspecific variation of *P. kerrii* and interspecific variation of 462 tree species within the Xishuangbanna tropical seasonal rainforest.

| Traits | Intraspecific | | | Interspecific | | | Range covered (%) |
|--|---------------|------|---------------|---------------|------|--------------|---------------------|
| | Mean | CV | Range | Mean | CV | Range | |
| Leaf area (cm ²) | 74.61 | 0.24 | 40.45–120.80 | 31.94 | 3.53 | 1.86–239.53 | 33.80% |
| Specific leaf area (cm ² /g) | 146.23 | 0.13 | 110.90–194.90 | 56.67 | 0.72 | 14.48–394.34 | 22.11% |
| Leaf chlorophyll content (SPAD) | 59.30 | 0.10 | 48.26–75.02 | 50.02 | 0.15 | 24.98–67.12 | ^a 44.76% |
| Leaf thickness (mm) | 0.27 | 0.11 | 0.20–0.34 | 0.23 | 0.25 | 0.11–0.63 | 26.92% |
| Mass based leaf chlorophyll content (umol/g) | 10.32 | 0.11 | 7.61–12.25 | – | – | – | – |
| Leaf density (g/cm ³) | 0.26 | 0.13 | 0.19–0.37 | – | – | – | – |

CV, coefficient of variation.

^a The part of the range of intraspecific variation that exceeds the interspecific range was ignored to allow comparison; – no interspecific data for comparison.

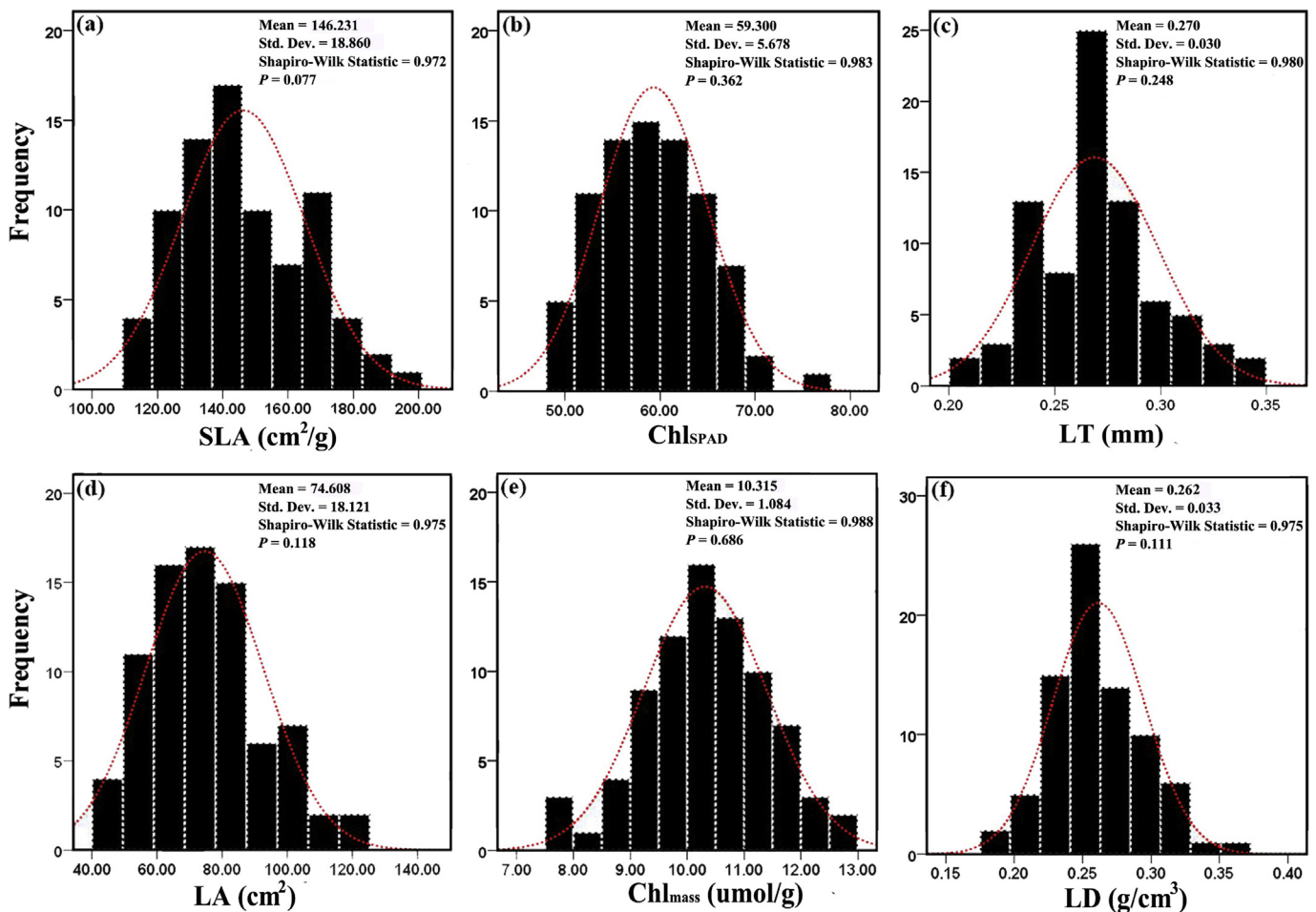


Fig. 1. The intraspecific trait variation of *P. kerrii* in the Xishuangbanna tropical seasonal rainforest in southwestern China. SLA, specific leaf area; Chl_{SPAD}, Leaf chlorophyll content, showed by SPAD value; LT, leaf thickness; LA, Leaf area; Chl_{mass}, mass based chlorophyll content; LD, leaf density.

of the interspecific variation of 462 tree species coexisting in the same community (Yang et al., 2014). *P. kerrii* is a highly abundant understory tree species within the Xishuangbanna tropical seasonal rainforest in southwestern China (Lan et al., 2008). This species is widespread in the tropical forests of Southeast Asia, such as those of Laos, Myanmar, Thailand, and North Vietnam (Peng and Howard, 2008; Hong and Stephen, 2015). We asked two questions: (1) How does intraspecific leaf trait variation of *P. kerrii* compare to the interspecific variation of mean trait values for most tree species in the same area? (2) Do *P. kerrii* leaf traits vary systematically with elevation?

2. Materials and method

2.1. Study site and focal species

Our study was established in a 20-ha (400 m × 500 m) Forest Dynamic Plot (FDP) (21°36'42"–85"N and 101°34'26"–47°00"E; Lan et al., 2008) and surrounding forest (approximately 4 km²) in the Xishuangbanna tropical seasonal rainforest in southwestern China. Rain forest canopy reached ca. 50 m (Zheng et al., 2006). The region is part of the Indo–Burma biodiversity hotspot (Myers et al., 2000). The annual rainfall within the Xishuangbanna tropical seasonal rainforest has an average of 1493 mm, of which ca. 1256 mm (84%) occurs between May to October; soil type is derived from siliceous rock (Cao et al., 2006).

P. kerrii is a small shade-tolerant tree species, 4–7 m tall, that inhabits dense valley forests with an elevation range of 300–1600 m and is mainly distributed in South Yunnan (China), Laos, Myanmar, Thailand, and North Vietnam. *P. kerrii* seeds are edible and used medicinally (Peng and Howard, 2008). *P. kerrii* is the most abundant tree species in the Xishuangbanna tropical seasonal rainforest, accounting for over 20% of the total individuals within the community. Other dominant tree species at the site are *Parashorea chinensis* H. Wang (Dipterocarpaceae) and *Garcinia cowa* Roxburgh (Clusiaceae) (Lan et al., 2008).

2.2. Intraspecific trait variation of *P. kerrii*

We measured leaf area (LA), specific leaf area (SLA), leaf thickness (LT), leaf density (LD), and leaf chlorophyll content (Chl) of three mature leaves from 80 individuals of *P. kerrii* within an area of approximately 4 km² in the Xishuangbanna tropical seasonal rainforest. Functional tradeoffs of these leaf traits between individuals and species have been described previously (Yang et al., 2014). Briefly, plants with high SLA usually have a fast resource acquisition and growth strategy, whereas plants with low SLA have a resource conservation and persistence strategy (Poorter et al., 2009). LT and LD, which are inversely related to SLA, can be calculated as $SLA = 1/(LT \times LD)$; therefore, increased LT or LD alone or simultaneously will lead to a decreased SLA (Poorter et al., 2009). Furthermore, leaf chlorophyll content is directly related to the photosynthetic rate of plants (Croft et al., 2017).

Because *P. kerrii* is a small shade-tolerant tree species, in most cases *P. kerrii* individuals do not receive direct light except for individuals in forest gaps. Therefore, to avoid the effects of sunlight, no *P. kerrii* individuals were selected within forest gaps. *P. kerrii* adults (generally with DBH > 3 cm and tree height > 4 m) were randomly sampled from valley to ridge habitat along elevation during the hot-dry season (April, 2015) to explore the elevation induced environment effects (e.g. water availability) on the leaf trait variation of *P. kerrii*. The elevation of each individual of *P. kerrii* sampled was determined by a hand-held GPS unit. Leaves were collected from the top of tree crowns without any obvious

symptoms of pathogen attack, herbivore attack, or substantial epiphylls cover (Cornelissen et al., 2003). Both LT (mm) and leaf chlorophyll content (Chl_{SPAD}) were measured in the field by an electronic digital micrometer (CANY Co., Shanghai, China) and a hand-held 'SPAD-502 Chl meter' (Minolta Camera Co., Osaka, Japan). Leaves were placed within a sealed plastic bag and taken to the laboratory immediately. LA (cm²) was measured using a leaf area meter (LI-COR 3100C Area Meter; LI-COR, USA). Each leaf was dried to a constant weight at 60 °C and weighed to the nearest 0.01 g (Cornelissen et al., 2003). SLA (cm² g⁻¹) was calculated as the ratio of LA to oven-dry leaf mass (LM, g). The SPAD value was converted to chlorophyll concentration per unit leaf area (Chl_{area}, μmol m⁻²) by $Chl_{area} = -112.9 + (13.9 \times Chl_{SPAD})$ (Anten and Hirose, 1999; Poorter and Bongers, 2006). The chlorophyll concentration per unit leaf mass (Chl_{mass}, μmol/g) was calculated as $Chl_{mass} = Chl_{area} \times (SLA / 10,000)$. LD (g cm⁻³) was calculated by $LD = LM / (LA \times LT / 10)$ (Witkowski and Lamont, 1991). Trait values were averaged for the three leaves collected within an individual of *P. kerrii*.

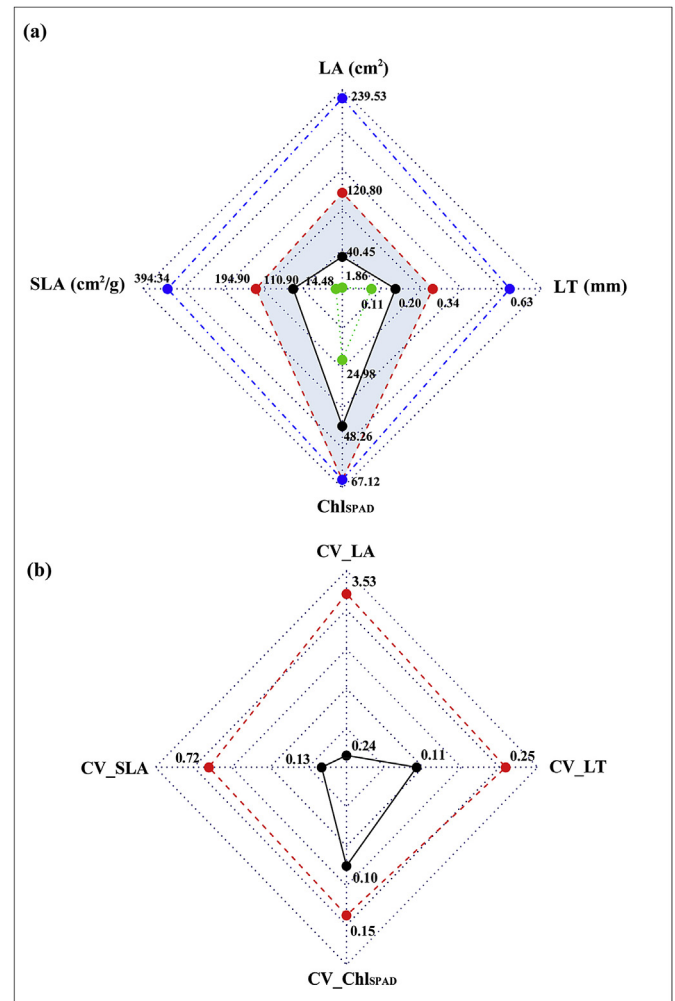


Fig. 2. Radar chart showing (a) the intraspecific trait variation, and (b) the coefficient of trait variation (CV) for four traits in *P. kerrii* and of 462 tree species in the Xishuangbanna tropical seasonal rainforest. In Fig. 2a, green and blue dots show the trait limits of interspecific variation of the 462 tree species (n = 462), black and red dots show the trait limits of the intraspecific variation of *P. kerrii* (n = 80). The shallow blue area shows the intraspecific trait variation of the four leaf traits of *P. kerrii*. In Fig. 2b, black dots show the CV (coefficient of variation) of leaf traits of *P. kerrii* and red dots show the CV of leaf traits of 462 tree species in the same area. This figure was generated using the function "radarchart" in the R package "fmsb" (Nakazawa, 2018).

2.3. Interspecific trait variation

Interspecific trait variation of 462 tree species (taxa) was first published in Yang et al. (2014), which includes most tree species in the study area. More than five leaves were sampled from each of five individuals of each taxon. LA, SLA, LT and Chl_{SPAD} were measured as described above and averaged for each species. For more details, see Yang et al. (2014).

2.4. Statistical analysis

Two indexes were calculated to show the intra- and interspecific trait variation. One is the range of trait variation and the other is the coefficient of variation (CV), which is calculated as $CV = \frac{SD}{M}$, where SD is standard deviation and M is mean (Fajardo and Piper, 2011). Shapiro–Wilk tests were used to evaluate the normality of variables investigated in this study (leaf functional traits and elevation) and all variables were found to be acceptably normal ($P > 0.05$). Pearson correlation analysis was used to test the correlations among the traits and linear regression analysis was used to test the effects of elevation on leaf traits. Significance was obtained at $P < 0.05$. These tests were implemented using SPSS 16.0 (SPSS Inc., Chicago, USA).

3. Results

3.1. Intraspecific trait variation of *P. kerrii* and interspecific trait variation of 462 tree species

Intraspecific variation of *P. kerrii* was substantial (Table 1; Fig. 1). LA varied threefold, ranging from 40.45 to 120.80 cm². SLA varied from 110.90 to 194.90 cm² g⁻¹. LT varied from 0.20 to 0.34 mm and leaf chlorophyll content, as shown by SPAD value (Chl_{SPAD}), varied

from 48.26 to 75.02. The coefficient of variation (CV) of *P. kerrii* leaf traits varied from 0.10 to 0.24.

The interspecific trait variation of 462 tree species is shown in Table 1. LA varied from 1.86 to 239.53 cm², SLA varied from 14.48 to 394.34 cm² g⁻¹, LT varied from 0.11 to 0.63 mm and Chl_{SPAD} varied from 24.98 to 67.12. The CV of these leaf traits varied from 0.15 to 3.53. The ranges of intraspecific trait variation of *P. kerrii* were 22.11%–44.76% of the ranges of interspecific trait variation among 462 tree species (Table 1, Fig. 2).

3.2. Trait correlations and variation of *P. kerrii* along elevation

Most leaf traits of *P. kerrii* were significantly correlated (Fig. 3). For example, LT and LD were negatively correlated with one another ($r = -0.441$, $P < 0.001$) and also negatively correlated with SLA ($r = -0.430$, $P < 0.001$; $r = -0.600$, $P < 0.001$). Chl_{mass} was positively correlated with SLA ($r = 0.572$, $P < 0.001$), while negatively correlated with LD ($r = 0.415$, $P < 0.001$). LA was positively correlated with LT but negatively correlated with LD ($r = 0.347$, $P = 0.002$; $r = -0.456$, $P < 0.001$). LT and LD increased, and SLA decreased significantly with increasing elevation (Fig. 4).

4. Discussion

4.1. Intraspecific variation is not negligible

Our study indicates that intraspecific variation in leaf traits is substantial. This finding is consistent with previous studies (Fajardo and Piper, 2011; Laforest-Lapointe et al., 2014; Siefert et al., 2015; Umana et al., 2015; Luo et al., 2016). For example, previous work has shown that the size of within-species variation is comparable with that of species-level variation (Messier et al., 2010). Furthermore, intraspecific variation has been found to account for 25% of the total trait variation within communities and 32% of the total trait

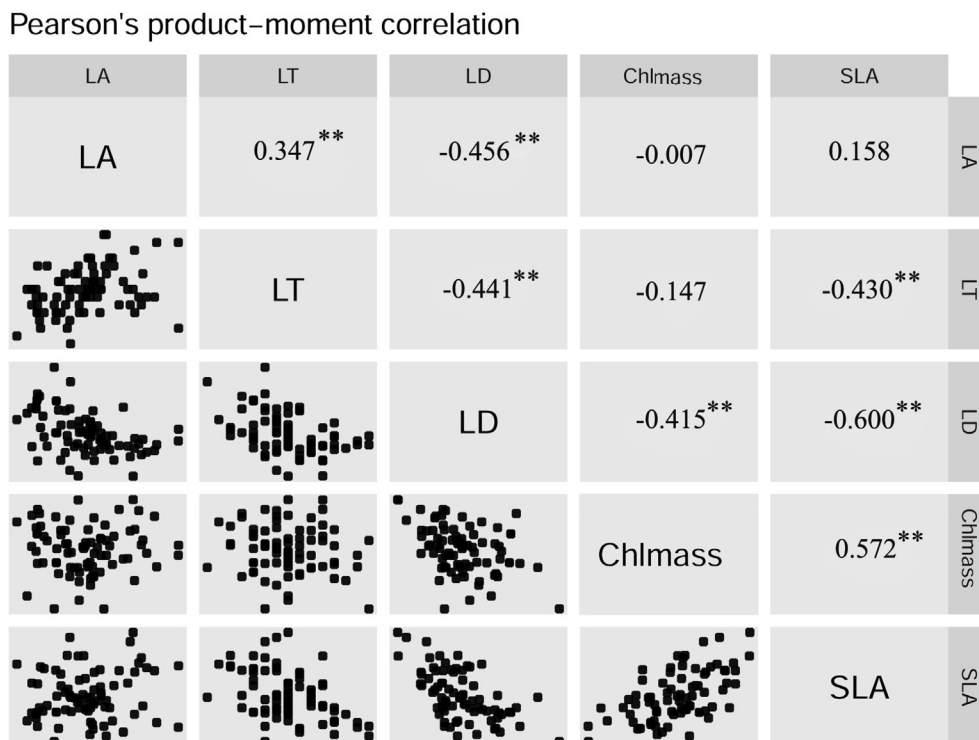


Fig. 3. Correlations between leaf traits of *P. kerrii* within the Xishuangbanna tropical seasonal rainforest. The data shown in the figure are the Pearson correlation coefficient. ** $P < 0.01$. This figure generated by function ggcorplot in the R package “Deducer” (Fellows, 2012; R Core Team, 2017).

variation among communities on average (Siefert et al., 2015). Together, these findings show that using a simple mean value for a functional trait ignores substantial trait variation at the intraspecific level.

4.2. Intraspecific trait correlations of *P. kerrii*

We found that various *P. kerrii* leaf traits were significantly correlated (Fig. 3). For example, SLA was negatively correlated with LT and LD but positively correlated with Chl_{mass} . SLA is a key trait that represents a functional tradeoff between growth and persistence for plant individuals or species (Sterck et al., 2006; Poorter et al., 2009). According to the resource availability hypothesis, plants in an environment with high resource availability invest more in growth than in persistence (Coley et al., 1986); therefore, the variation of SLA along with LT, LD and Chl_{mass} can be taken as the consequences of the individuals of *P. kerrii* to adapt to the diverse environment.

We also found that LD was negatively correlated with Chl_{mass} , indicating that denser leaves have a low mass-based content of chlorophyll, and chlorophyll content is directly related to the photosynthetic rate of plants (Croft et al., 2017). This is consistent with the discussions above that plants with denser leaves may invest more to persistence than to growth. Finally, we observed a significant positive correlation between LA and LT, which may indicate that LT plays a key role in determining the physical strength of leaves and thicker leaves are needed to support larger leaf area (Pérez-Harguindeguy et al., 2013).

4.3. Intraspecific trait variation along elevation

Plant traits are generally correlated with elevation (Read et al., 2014). For example, SLA is observed to decrease when elevation increases (Cordell et al., 1998; Hovenden and Vander Schoor, 2004; Fajardo and Piper, 2011; Laforest-Lapointe et al., 2014). Elevation may affect air temperature and in turn affect plant functional traits that help plants cope with colder environments at higher elevations (Fajardo and Piper, 2011). However, elevation may also affect other environmental properties (e.g. soil water content, light and nutrient availability) that affect plant traits (Markesteijn et al., 2010). In this study, both LD and LT increased, and SLA decreased significantly as elevation increased (Fig. 4); however, SLA varied along elevation more significantly than LT and LD. According to Poorter et al. (2009), SLA can be calculated as $\text{SLA} = 1/(\text{LT} \times \text{LD})$; therefore, SLA decreased when LT and LD increased alone or simultaneously. Thus, the more significant correlation between SLA and elevation could be a consequence of the simultaneous variation of LT and LD of *P. kerrii* in the Xishuangbanna tropical seasonal rainforest.

The elevational gradient within our study is relatively small (703–824 m); however, even within this elevational gradient, the intraspecific variation of *P. kerrii* leaf traits, is substantial and correlates with elevation (Figs. 1 and 4). A probable explanation for these patterns is that changes in environmental correlates are associated with topography. Within a relatively small elevational gradient, the effects of elevation on temperature could be small, whereas other factors, such as soil water and nutrient availability, could be significantly different. For instance, in the Xishuangbanna tropical seasonal rainforest, pH, phosphorous availability, and soil water availability are higher in valley habitats than in slopes or ridges at relatively higher elevations (Zheng et al., 2006; Xu et al., 2016). Water stress differences are especially pronounced in the hot-dry season (from March to April) (Cao et al., 2006). Again, in order to tolerate environmental stresses at higher elevations (e.g. soil water availability) in the Xishuangbanna tropical seasonal rainforest, it may be more beneficial for *P. kerrii* individuals to

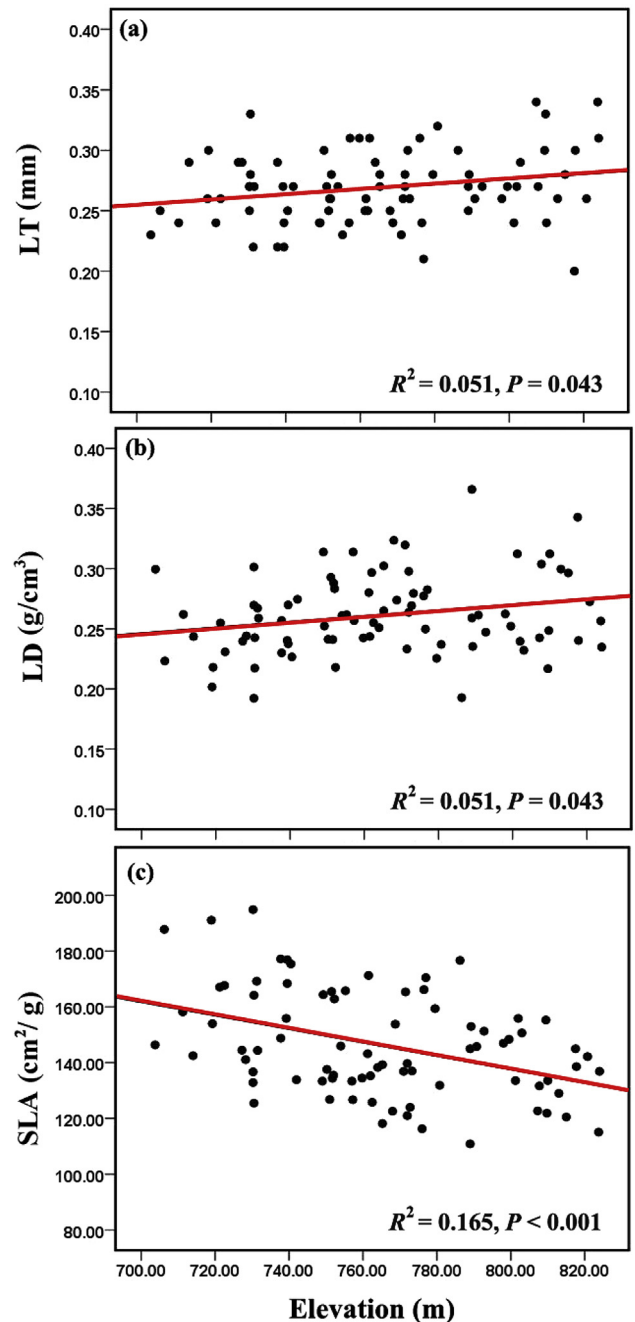


Fig. 4. Variations in leaf thickness, density and specific leaf area of *P. kerrii* along an elevational gradient. R^2 is the coefficient of determination in linear regression analysis. SLA, specific leaf area; LT, leaf thickness; LD, leaf density.

produce thicker and denser leaves rather than to increase growth rates (Fig. 4). Notably, we only investigated intraspecific variation of *P. kerrii*, the most abundant tree species; however, it has been shown that common species shown less intraspecific trait variation than rare species in the Xishuangbanna tropical seasonal rainforest because rare species are more likely struggling for success in a given environment (Umana et al., 2015).

5. Concluding remarks

Is intraspecific variation negligible? Our study indicates that intraspecific variation is substantial and should not be ignored. Intraspecific variation may help species adapt to diverse

environments and pass through biotic and abiotic filters. Our study provides support for a shift from species-based to individual-based community ecology (Violle et al., 2012).

Declaration of Competing Interest

The authors declare no conflict of interests.

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