



## Original article

# Twig–leaf size relationships in woody plants vary intraspecifically along a soil moisture gradient



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## ARTICLE INFO

## Article history:

Received 9 January 2014

Accepted 30 July 2014

Available online

## Keywords:

Allometric scaling

Individual variability

Interspecific variability

Isometric scaling

Overlapping species

Total leaf area

Twig cross-sectional area

Variance partition

## ABSTRACT

Understanding scaling relationships between twig size and leaf size along environmental gradients is important for revealing strategies of plant biomass allocation with changing environmental constraints. However, it remains poorly understood how variations in the slope and *y*-intercept in the twig–leaf size relationship partition among individual, population and species levels across communities. Here, we determined the scaling relationships between twig cross-sectional area (twig size) and total leaf area per twig (leaf size) among individual, population and species levels along a soil moisture gradient in subtropical forests in eastern China. Twig and leaf tissues from 95 woody plant species were collected from three sites that form a soil moisture gradient: a wet site (W), a mesophytic site (M), and a dry site (D). The variance in scaling slope and *y*-intercept was partitioned among individual, population and species levels using a nested ANOVA. In addition, the change in the twig–leaf size relationship over the soil moisture gradient was determined for each of overlapping and turnover species. Twig size was positively related to leaf size across the three levels, with the variance partitioned at the individual level in scaling slope and *y*-intercept being 98 and 90%, respectively. Along the soil moisture gradient, the twig–leaf size relationship differed inter- and intraspecifically. At the species and population levels, there were homogeneous slopes but the *y*-intercept was  $W > M = D$ . In contrast, at the individual level, the regression slopes were heterogeneous among the three sites. More remarkably, the twig–leaf size relationships changed from negative allometry for overlapping species to isometry for turnover species. This study provides strong evidence for the twig–leaf size relationship to be intraspecific, particularly at the individual level. Our findings suggest that whether or not species have overlapping habitats is crucial for shaping the deployment pattern between twigs and leaves.

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## 1. Introduction

The twig size–leaf size relationship is one of the leading dimensions in plant ecological strategies (Westoby et al., 2002). Twig cross-sectional area (twig size) and total leaf area per twig (leaf size) of woody plants are expected to be coordinated for mechanical and hydraulic reasons. Since the twig–leaf size scaling relationship links closely with the plant's water and carbon use

efficiencies (Olson et al., 2009), this relationship is critical for shaping plant leaf and wood economics, and plant architecture and functioning (Niklas, 1994; Niklas and Enquist, 2002; Westoby et al., 2002; Ogawa, 2008). Although the twig–leaf size relationship, or the Corner's rule, was introduced more than half a century ago (Corner, 1949), there has been reinvigorated research interest in analyzing how the twig–leaf size scaling relationship varies with environmental factors (Westoby and Wright, 2003; Sun et al., 2006; Yang et al., 2009), plant ontogeny (Ackerly and Donoghue, 1998; Preston and Ackerly, 2003), or taxonomic groups (White, 1983a,b; Brouat et al., 1998; Normand et al., 2008).

The scaling slope and *y*-intercept in the linear log–log twig–leaf size relationship can be used to describe plant biomass allocation

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between twigs and leaves in response to environmental constraints. Scaling slopes greater or less than 1 indicate two related but contrasting allometric relationships, reflecting different strategies of resource allocation in plants (Niklas, 1994). Contrary to allometric relationships, scaling relationships with a slope equal to 1 indicate that one unit increase in twig size causes a proportional increase in leaf size. Also, under the precondition of homogeneous slope, a shifting pattern of the  $y$ -intercept in the twig–leaf size relationship along environmental gradients indicates how plants cope with environmental constraints in their leaf size deployment at a given twig size (Westoby and Wright, 2003; Sun et al., 2006).

An environmental gradient may be seen as a natural source of expected variation in the twig–leaf size relationship. It is well known that variations in xylem structure and hydraulic architecture of plants are linked with gradients in water availability in habitats (Villar-Salvador et al., 1997; Cavender-Bares and Holbrook, 2001). Since twig and leaf sizes are two key elements for shaping plants' hydraulic architecture, the twig–leaf size relationship presents a life history trade-off between efficiency and safety in the hydraulic transport of water (Sun et al., 2006). Specifically, for adding hydraulic transport and photosynthesis capability, plants are expected to carry more total leaf area per twig in wetter than in drier habitats (Preston and Ackerly, 2003; Sun et al., 2006). This is understandable as water stress is less in wetter sites, so plants can afford to support a greater leaf area per twig. Conversely, in drier habitats, resistance to cavitation appears to be maximized at the expense of efficiency in water transport, so plants tend to deploy a smaller leaf area at a given twig size to reduce water evaporation and increase plant resistance to drought (Niklas, 1994; Sobrado, 1997; Preston and Ackerly, 2003; Westoby and Wright, 2003; Sun et al., 2006). Hence, it is expected that the scaling relationship between twig size and leaf size of plants may systematically change along a soil moisture gradient.

Although the empirical evidence suggests that the scaling slope in the twig–leaf size relationship is invariant along a soil moisture gradient, past research on the scaling slope has been focused mainly on patterns across species (Ackerly and Donoghue, 1998; Preston and Ackerly, 2003; Westoby and Wright, 2003). Currently, we don't fully understand how twig–leaf size relationships differ intraspecifically along a soil moisture gradient (Normand et al., 2008). At the plant community level, intraspecific variability of the twig–leaf size relationship may be derived from three main components: i) population-level variability: the difference between populations of a species; ii) variability between individuals within a given population; and iii) variability within an individual (Albert et al., 2011; Bolnick et al., 2011). Unfortunately, it remains poorly understood how variations in the slope and  $y$ -intercept in the twig–leaf size relationship partition among individual, population and species levels. We also do not have a good understanding of whether the pattern of twig–leaf size relationship along a soil moisture gradient is consistent among individual, population and species levels.

The twig–leaf size relationship along a soil moisture gradient may also differ between overlapping species and turnover species. Overlapping species are defined here as species that appear in more than one habitat. Species that appear only in one habitat are defined as turnover species. The comparison of overlapping and turnover species in their twig–leaf size relationship along a soil moisture gradient will help understand the variations while controlling phylogenetic inertia. We predict that, the twig–leaf size relationship along a soil moisture gradient will be different between overlapping and turnover species, because turnover and overlapping species have different responses in their ecological strategies to environmental changes (Geber and Griffen, 2003; Messier et al., 2010; Fajardo and Piper, 2011; McGlenn and Hurlbert, 2012).

The objective of this study was to investigate the variation in the twig–leaf size relationship among individual, population and species levels using 95 woody plant species in three sites that form a soil moisture gradient in subtropical evergreen forests in eastern China. We predict that: 1) the twig–leaf size scaling relationship varies across three sites; 2) variance partitioning in the slope and  $y$ -intercept in the twig–leaf size relationship among individual, population and species levels will have a large intraspecific component (*i.e.*, individuals plus populations); and 3) overlapping and turnover species have dissimilar scaling relationships.

## 2. Materials and methods

### 2.1. Study area, forests and plant species

This study was conducted in the Tiantong National Forest Park and surrounding area (29°41'–50'N, 121°36'–52'E), situated on the lower eastern extension of the Siming Mountain, Zhejiang Province, Eastern China. The highest peak in this area was at 653 m above sea level, while the height of most other peaks ranged between 70 and 300 m. The area has a typical monsoon climate with a hot, humid summer and a drier cold winter (Yan et al., 2009). The zonal vegetation in this region is subtropical evergreen broad-leaved forests (EBLFs), which had been severely disturbed by human impact in the history with only small tracks of intact or semi-intact EBLFs left around a Buddhist temple in the Tiantong National Forest Park. The mature and secondary EBLFs usually occurred in mesophytic habitats (M). In the wet ravine area (W), the mature forest was mixed between evergreen and deciduous species. Outside of the park, the habitats were relatively dry (D) and virtually all vegetation were secondary EBLFs shrubs caused by clear-cutting in the earlier years. In this study, these site types were selected to represent a soil moisture gradient. The details of the site properties are given in Table 1.

In order to characterize the pattern of twig–leaf size scaling along this soil moisture gradient, we established six plots at the W site, eighteen plots at the M site, and seven plots at the D site with the same aspect and slope to the best extent possible. Each plot (20 × 20 m) was located at least 100 m from the stand edge. All woody plant species present in each plot were sampled. The total number of species sampled was 95, belonging to 31 families and 69 genera, including 916 individual trees and shrubs, with 50, 64, and 30 species sampled in the W, M and D sites, respectively. There were 27, 22 and 8 overlapping species for each of the M–W, M–D and W–D pairs, respectively, and 7 overlapping species across the three sites. The species are listed in Table A1. Since differences in leaf habit may contribute to variations in the twig–leaf size relationship (*e.g.*, Cavender-Bares and Holbrook, 2001), it should be noted that the proportion of evergreen vs. deciduous species was different among the three sites. The community importance value of deciduous species in the W, M and D sites was 40, 5 and 20%, respectively.

### 2.2. Twig and leaf data collection

In each plot, twig and leaf samples were collected from each individual plant in July and August of 2008. For each individual, five branches were cut from five different positions, *i.e.*, the four directional canopy brims and the upper position of the crown. In the field, current year twigs were separated from the branch immediately after being collected based on the location of internodes. We assumed that twig growth for the current year was over for all species by the time of sample collection, so the current year shoot was defined here as a twig. From each branch, one twig without apparent leaf loss and/or damage was chosen, stored in a

**Table 1**

Characteristics of three sites that form a soil moisture gradient in Tiantong National Forest Park and surrounding areas in eastern China. Soil moisture content, soil bulk density and soil pH were measured from fresh mineral soil samples of 0–20 cm depth. Different lowercase letters in each row indicate significant differences among sites (adjusted  $P < 0.05$ ). Data are means  $\pm$  SE.

Site properties	Dry site	Mesophytic site	Wet site
Air humidity (%)	71.1 $\pm$ 4.3 a	78.1 $\pm$ 1.7 b	87.2 $\pm$ 2.4 c
Soil moisture content (%)	16.2 $\pm$ 1.5 a	21.9 $\pm$ 2.4 b	29.6 $\pm$ 3.7 c
pH (2:1 H <sub>2</sub> O)	4.2 $\pm$ 0.08 a	4.2 $\pm$ 0.05 a	3.8 $\pm$ 0.07 b
Soil bulk density (g cm <sup>-3</sup> )	1.3 $\pm$ 0.04 a	1.3 $\pm$ 0.04 a	1.1 $\pm$ 0.06 b
Elevation (m)	200 $\pm$ 52 a	300 $\pm$ 61 a	260 $\pm$ 38 a
Vegetation type	Secondary shrub	Evergreen broad-leaved forest	Evergreen and deciduous mixed forest
Community structure			
Number of vertical layers	1	3	3
Canopy height (m)	5–7	18–22	18–24
Canopy cover (%)	70–74	80–82	90–92
Dominant species	<i>Schima superba</i> <i>Lithocarpus glabra</i> <i>Quercus fabric</i>	<i>Castanopsis fargesii</i> <i>Castanopsis carlesii</i> <i>Schima superba</i>	<i>Choerospondias axillaris</i> <i>Liquidambar formosana</i> <i>Machilus leptophylla</i>

zip-lock bag and kept cool until it was brought back to the laboratory for measurement, which was usually performed within 12 h of sample collection. In the laboratory, the leaf and stem were separated for each twig. Then twig diameter at the base of the lowest live leaf along the length was measured. Twig diameter was measured twice (at two angles perpendicular to each other) using an electronic vernier caliper (accurate to 0.1 mm). Twig cross-sectional area was calculated from the diameter. At the same time, all leaves from each twig were scanned using a leaf area meter (LI-3100C, Li-Cor, USA) to determine the leaf area. Here, we used twig cross-sectional area to represent twig size, and total leaf area per twig to represent total leaf size per twig.

### 2.3. Data analysis

#### 2.3.1. Variance decomposition of the twig–leaf size scaling and the twig and leaf traits among individual, population and species levels

Population is defined here as all individuals of a given species within a given plot. We assessed variation in twig–leaf size relationship across three levels: 1) across individuals within a population; 2) across populations within a species; and 3) across species. For subsequent analyses, variances of the individual-level value and the population-level value in twig–leaf size scaling of a given species were considered as the intraspecific variability. The variance at species-level in a given site was recognized as the inter-specific variability.

To determine the slope and intercept for twig–leaf size scaling, the log–log relationship between twig size and leaf size was analyzed using standardized major axis (SMA) regression. Regression procedures were carried out using (S)MATR (Version 2.0, Falster et al., 2006, <http://www.bio.mq.edu.au/ecology/SMATR/>). In this software, confidence intervals for scaling slopes were calculated following Pitman (1939). The heterogeneity of regression slopes and common slopes among groups was calculated following Warton and Weber (2002). Differences in the y-intercept and shifts against the common slope were tested by the post hoc Tukey test in ANOVA.

In the first step, twig and leaf sizes of the five twigs for each individual of each species within each plot were used to fit a linear regression equation. In total, we computed 916 scaling slopes and y-intercepts for all individual plants. Then these 916 results were hierarchically structured at individual, population and species levels. After this, a hierarchical ANOVA was carried out to decompose variance among individual, population and species levels. In this case, we fitted a general linear model to the scaling variance among the three levels with a nested ANOVA with random effects in the increasing order of individual, population, and species, by using a restricted maximum likelihood (REML) method in the

'lme4' package of R (version 2.11.1). In this procedure, a variance component analysis was performed using the 'ape' package of R (R Development Core Team, 2009).

Finally, a nested ANOVA was conducted further to decompose variance for twig and leaf sizes into individual, population and species levels to evaluate variance partitioning patterns among the three levels.

#### 2.3.2. Analysis of scaling variability among individual, population and species levels

To determine whether the pattern of twig–leaf size scaling along the soil moisture gradient remains consistent across the three levels, we conducted SMA regression analysis separately at each of individual, population, and species level to calculate the respective scaling slope and y-intercept. Firstly, twig and leaf sizes of five twigs per individual were averaged arithmetically, and then the twig–leaf size relationship was analyzed for the individual level. For the population level, twig size and leaf size of individuals were averaged arithmetically for each population, then the SMA regression was conducted across populations for each species. For the species level, twig size and leaf size for the populations of each species were averaged arithmetically, then regression across species was conducted.

In each of the above three SMA regressions, the heterogeneity of regression slopes among the three sites was tested through re-sampling and permutation procedures (Warton et al., 2006). When slopes did not differ among sites, differences in the y-intercept were tested by the Wald test available in (S)MATR. After this, the patterns in 'individual-level value', 'population-level value' and 'species-level value' along the soil moisture gradient were compared.

#### 2.3.3. Analysis of scaling variability between overlapping and turnover species

In order to investigate whether overlapping and turnover species generate similar scaling relationships along the soil moisture gradient, we repeated the SMA regression procedures for each of overlapping and turnover species at each of individual, population, and species level. Then the pattern of twig–leaf size scaling was compared between overlapping and turnover species.

## 3. Results

### 3.1. Variance partitioning of twig–leaf size scaling among individual, population and species levels

The variance partitioning of the slope and y-intercept in twig–leaf size relationships was unequal among the three levels,

**Table 2**

Variance partitioning among individual, population and species levels based on the full nested linear models in scaling relationships between twig cross-sectional area and total leaf area: 1) slope, 2) intercept, 3) total leaf area, and 4) twig cross-sectional area. The scaling was performed using the log–log standardized major axis regression analysis.  $n = 916$  individual trees and shrubs. Values are means and 95% confidence intervals of 500 runs. The confidence intervals were calculated by bootstrapping, with 500 runs and 700 randomly sampled data points with replacement.

Level	% Variance of scaling		% Variance of trait	
	Slope	Intercept	Total leaf area	Twig cross-sectional area
Individual and error	98 (91–100)	90 (82–98)	29 (17–36)	19 (17–22)
Population	1 (0–9)	8 (0–19)	25 (18–44)	9 (7–12)
Species	1 (0–3)	2 (0–6)	46 (41–55)	72 (69–75)

with the major part of variance occurring among individuals (Table 2). The variance component among individuals was 98 and 90% for the slope and  $y$ -intercept, respectively, with the remaining variance contributed by populations and species (Table 2). It should be noted that the residual error was pooled at the individual level. This might affect the variance partitioning for the scaling slope and intercept.

The variance partitioning pattern was different between twig size and leaf size. The variance for total leaf area was roughly evenly distributed between inter- and intra-species levels, whereas for twig cross-sectional area, the variance component related to inter-specific differences was significantly larger at species than at population and individual levels (Table 2).

### 3.2. Variation in twig–leaf size relationship along the soil moisture gradient

When overlapping and turnover species were combined together, the twig cross-sectional area was positively related with total leaf area across the three sites. At the species and population levels, the slope was not different between any two sites ( $P > 0.05$ ; Fig. 1d, h), and a common regression slope could be calculated (Fig. 1a, e). However, the  $y$ -intercept was different among the sites ( $P < 0.001$ ), being  $W > M = D$  (Fig. 1a, e). In contrast, at the individual level, the slope was heterogeneous among sites, differing significantly between M and D and between M and W (Fig. 1i, l) ( $P < 0.05$ ).

### 3.3. Variation in twig–leaf size relationship between overlapping and turnover species

The regression slope did not differ and was homogeneous for overlapping and turnover species, respectively, at (Fig. 1b, c), population (Fig. 1f, g) and individual (Fig. 1j, k) levels. However, the common slope differed significantly between overlapping and turnover species. The scaling relationship between twig size and leaf size was a negative allometry for overlapping species (Fig. 1b, f, j), but an isometry for turnover species (Fig. 1c, g, k) at individual, population and species levels. The  $y$ -intercept in the twig–leaf size relationship was contrasting between overlapping and turnover species. At the species level, the  $y$ -intercept did not shift between any two sites for overlapping species (Fig. 1b), but was greater in W than in M and D for turnover species (Fig. 1c). At the levels of population and individual, the  $y$ -intercept was greater in W and M than in D for overlapping species (Fig. 1f, j), but did not differ among sites for turnover species (Fig. 1g, k).

## 4. Discussion

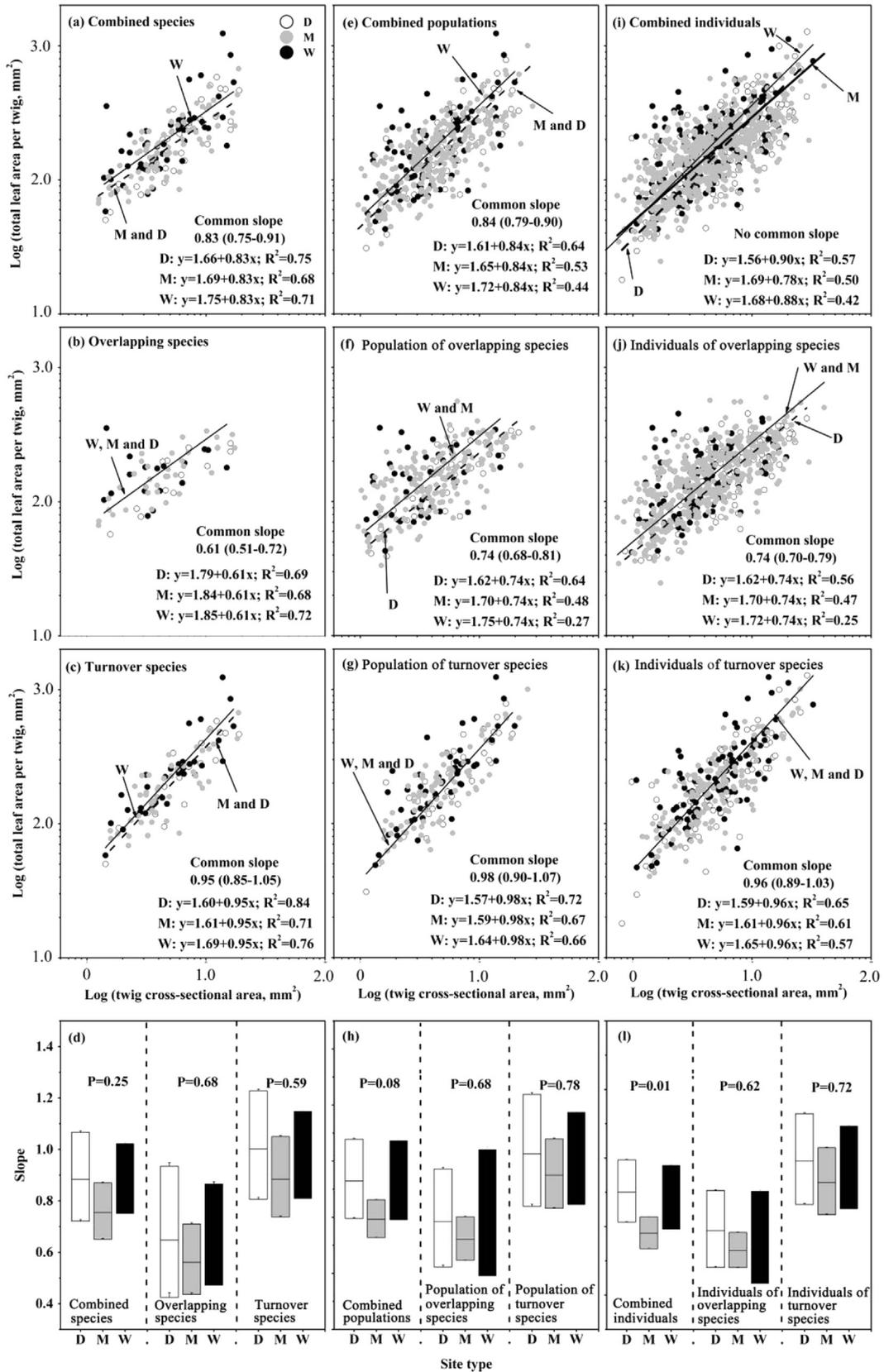
### 4.1. Individual variability of the twig–leaf size relationship along a soil moisture gradient

The fact that most of the variance of the slope and intercept in the twig–leaf size relationships were at the individual level (Table 2) illustrates the individual-based variability of the twig–leaf size relationship, which was also demonstrated by the contrasting patterns of the twig–leaf size scaling relationship among individual, population and species levels along the soil moisture gradient (Fig. 1). Therefore, the first and second predictions in this study are supported by our results.

The greatest variance partition in the twig–leaf size relationship at the individual level suggests a substantial amount of variation across individual plants. Individual variability of the twig–leaf size relationship may be associated with many aspects of development, physiology, and life history, and may also be related to environmental constraints (Schlichting, 1986; Ackerly and Donoghue, 1998; Bolnick et al., 2003; Preston and Ackerly, 2003; Sultan, 2004). For example, it can be caused by spatial heterogeneity of twig and leaf traits within a tree crown (e.g., sun vs. shade leaves and associated twigs). In this study, we found that individual variation in total leaf area and twig cross-sectional area accounted for 29 and 19%, respectively, of the total variation (Table 2). The unequal variability of these two traits at the individual level, hence, might contribute to the substantial variation in their relationship. In addition, the individual variability of the twig–leaf size relationship can be caused by plant ontogeny. Although this study did not standardize (or control) for ontogeny by sampling both adults and saplings, it is very probable that plant ontogenetic variation may also affect the twig–leaf size relationship, because ontogenetic variability is closely related to plant architecture and hydraulic constraints that shape plant leaf and wood economies (Ackerly and Donoghue, 1998; Preston and Ackerly, 2003; Fajardo and Piper, 2011).

At the individual level, the scaling slope was heterogeneous among the three sites (Fig. 1j). Although scaling slopes among the three sites were consistently less than 1 (i.e., negative allometry), it was statistically smaller in M than in W and D sites ( $P < 0.01$ ). The twig–leaf size scaling relationship with slopes greater in W and D than in M implies that, at a given unit of increase in twig size, the rate of increase of leaf size was greater in W and D than in M sites, likely caused by different biomass allocation strategies for individual plants among the three sites with differing soil water availability and plant competition. In the W sites, in order to deal with the excessive moisture availability, plants that tolerate long periods of wetness might have efficient hydraulic transport and large rates of transpiration at the expense of mechanic safety (Ackerly and Donoghue, 1998; Preston and Ackerly, 2003; Fajardo and Piper, 2011). Therefore, plants tend to develop more leaf area at a given rate of increase of twig size (Normand et al., 2008). In this way, they can transpire a significant amount of water daily. In contrast, in the D sites, although water availability was low, the competition for vertical growth becomes strong because the dominant plants were secondary shrubs in this study. To win the competition, plants would invest more biomass in leaves at a given unit of increase of twig size through expanding leaf area to capture more light (Olson et al., 2009). This strategy might lead to a greater scaling slope in the twig–leaf size relationship in the D than in the M sites.

At the species and population levels, scaling slopes were homogeneous while  $y$ -intercepts differed among the three sites that formed the soil moisture gradient, consistent with previous reports (Westoby and Wright, 2003; Sun et al., 2006; Normand et al., 2008; Yang et al., 2009). In this study, the  $y$ -intercept of the twig–leaf size



**Fig. 1.** Scaling relationships between (log) twig cross-sectional area and (log) total leaf area for 95 woody plant species (916 individuals) found in three sites differing in soil moisture regime in subtropical forests in eastern China. The regression relationship is presented for: (a) combined species (overlapping and turnover species combined), (b) overlapping species, (c) turnover species, (e) combined populations (overlapping and turnover populations combined). Overlapping and turnover populations are defined here as populations within each of the overlapping and turnover species), (f) population of overlapping species, (g) population of turnover species, (i) combined individuals (individuals in both overlapping and turnover species combined), (j) individuals of overlapping species, and (k) individuals of turnover species. The regression slope, 95% confidence interval (CI) and significance for testing slope heterogeneity for each of individual population species, and level are presented in (d), (h) and (i), respectively. Within each graph, the lines are the reduced major axis regression curves, and the common slope (CI) and regression equations are also given. The symbols in each graph represent site types: D: dry site; M: mesophytic site, and W: wet site.

relationship was the highest in the wet site and the lowest in both the dry and mesophytic sites at the population and species levels (Fig. 1a, e), suggesting that at a given twig cross-sectional area, plants in wet habitats support more total leaf area than those in dry and mesophytic habitats, as a result of different hydraulic responses to soil moisture availability (Preston and Ackerly, 2003; Westoby and Wright, 2003; Sun et al., 2006). In contrast, plants tend to deploy a smaller leaf area at a given twig size in drier habitats to reduce transpiration demand and to increase resistance to drought (Niklas, 1994; Sobrado, 1997; Preston and Ackerly, 2003; Westoby and Wright, 2003; Sun et al., 2006).

#### 4.2. Variability of the twig–leaf size relationship between overlapping species and turnover species along a soil moisture gradient

It is well known that most of the variation in plant traits and the trait–trait relationships among sites might be caused by both species that overlap or turnover (Coleman et al., 1994; Cornwell and Ackerly, 2009). It is the case in this study that overlapping and turnover species generated different patterns in their twig–leaf size relationships across the three sites (i.e., supporting the third prediction). In this study, the dissimilar scaling slopes between overlapping and turnover species suggest that the twig–leaf relationship is largely dependent of the ability of the species to overlap habitats or not. The isometric relationships in turnover species among the three sites indicate that leaf size always increases with stem size at a constant and proportional rate, regardless of soil moisture availability. The mechanisms underlying this isometric relationship might be attributable to developmental correlations between twigs and leaves, which might limit the ability of each organ to evolve an independent response (Watson and Casper, 1984; Harvey and Pagel, 1991; Niklas, 1994).

In contrast, the invariant negative allometric relationships in overlapping species indicate that plant species with large intraspecific variability between overlapping habitats tend to deploy small leaf area at a given twig size. The intraspecific variability of overlapping species in the twig–leaf size relationship might be related to their phenotypic plasticity in response to changing soil moisture conditions. Acclimation or phenotypic plasticity allows each genotype to produce multiple phenotypes under different environmental conditions (DeWitt et al., 1998; Geber and Griffen,

2003). Therefore, overlapping species with a strong phenotypic plasticity display dissimilar patterns in their twig–leaf deployment, as compared to the turnover species. The functional equivalence hypothesis may be applied for interpreting the phenotypic plasticity of the twig–leaf size relationship in overlapping species. Brouat and McKey (2001) stated that leaf–stem size correlations are not always constrained but variable. Although the cost and benefit behind the negative allometric relationship is not clear for overlapping species, we speculate that fundamental trade-offs between efficiency and safety of plant hydraulic transportation might be one of the mechanisms driving the negative allometric relationship between twigs and leaves. This mechanism should be directly tested in future research.

## 5. Conclusions

The variance components of scaling slope and y-intercept in the twig–leaf size relationship were not evenly distributed among individual, population and species levels. The slope and intercept of the scaling relationship vary much more strongly within than across species. The twig–leaf size relationships along a soil moisture gradient vary from negative allometry for overlapping species to isometry for turnover species, suggesting that whether or not the species occupy several different habitats is crucial for shaping the deployment pattern between twigs and leaves. We conclude that the variability of the twig–leaf size relationship was strongly intraspecific. Therefore, if a research is focused on variability of the twig–leaf size relationship along environmental gradients, the intraspecific variation should be accounted for.

## Acknowledgments

The authors thank Zhou Wu, Guo Min, Zhong Qiang, Kang Meng, Zeng Min, Zhou Zhou, Xu Zhaozhen, Cao Wenjuan, Lu Datong, Wen Yanjun, Chen Ying and Huang Jun for their help in the field and laboratory. This work was supported by the National Natural Science Foundation of China (Grant Nos. 31270475 and 31070383), and the Key Scientific and Technological Project of Ningbo City in China (Grant No. 2012C10027).

## Appendix A

**Table A1**

Leaf habit, plant growth form, twig and leaf sizes of 95 woody plant species among three sites differing in soil moisture contents in the subtropical evergreen broadleaved forests in eastern China (Mean  $\pm$  SD). EC, BD and BE are evergreen conifers, broad-leaved deciduous and broad-leaved evergreens species, respectively.

Habitat	Taxonomic family	Species (number of individuals sampled per species in all plots in each habitat)	Leaf habit	Plant growth form	Twig cross-sectional area (mm <sup>2</sup> )	Total leaf area per twig (mm <sup>2</sup> )
Dry	Pinaceae	<i>Pinus massoniana</i> (15)	EC	Trees	16.11 $\pm$ 5.64	272.49 $\pm$ 92.67
	Aquifoliaceae	<i>Ilex purpurea</i> (9)	BE	Trees	4.80 $\pm$ 0.86	209.32 $\pm$ 45.40
	Ebenaceae	<i>Diospyros kaki</i> var. <i>silvestris</i> (4)	BD	Trees	10.07 $\pm$ 2.49	367.36 $\pm$ 94.01
		<i>Rhododendron mariesii</i> (6)	BD	Shrubs	1.84 $\pm$ 1.37	92.91 $\pm$ 74.32
	Ericaceae	<i>Vaccinium sbracteatum</i> (7)	BE	Shrubs	4.54 $\pm$ 1.68	95.63 $\pm$ 36.25
	Euphorbiaceae	<i>Mallotus tenuifolius</i> (1)	BD	Trees	14.56	474.2
	Fagaceae	<i>Castanopsis sclerophylla</i> (2)	BE	Trees	4.33 $\pm$ 1.81	199.29 $\pm$ 49.72
		<i>Lithocarpus glaber</i> (2)	BE	Trees	2.85 $\pm$ 0.83	77.47 $\pm$ 15.72
		<i>Quercus fabri</i> (16)	BD	Trees	7.14 $\pm$ 2.37	249.71 $\pm$ 85.96
	Hamamelidaceae	<i>Liquidambar formosana</i> (9)	BD	Trees	12.29 $\pm$ 8.85	583.45 $\pm$ 364.67
		<i>Loropetalum chinense</i> (11)	BE	Shrubs	1.60 $\pm$ 0.75	58.73 $\pm$ 21.54
	Lauraceae	<i>Litsea cubeba</i> (3)	BD	Shrubs	18.97 $\pm$ 6.22	465.19 $\pm$ 207.93
	Leguminosae	<i>Albizia kalkora</i> (3)	BD	Trees	3.76 $\pm$ 0.57	117.59 $\pm$ 23.71
		<i>Dalbergia hupeana</i> (8)	BD	Trees	9.41 $\pm$ 3.72	288.92 $\pm$ 115.28
		<i>Lespedeza chinensis</i> (3)	BD	Shrubs	5.31 $\pm$ 0.81	337.17 $\pm$ 37.99
	Myricaceae	<i>Myrica rubra</i> (3)	BE	Trees	6.21 $\pm$ 2.50	158.58 $\pm$ 41.83
	Myrtaceae	<i>Syzygium buxifolium</i> (3)	BE	Shrubs	1.43 $\pm$ 0.15	50.15 $\pm$ 5.15
	Moraceae	<i>Ficus erecta</i> var. <i>beecheana</i> (2)	BD	Shrubs	10.81 $\pm$ 0.59	506.82 $\pm$ 121.37
	Rhamnaceae	<i>Rhamnus globosa</i> (3)	BD	Shrubs	4.14 $\pm$ 1.11	194.79 $\pm$ 20.09

Table A1 (continued)

Habitat	Taxonomic family	Species (number of individuals sampled per species in all plots in each habitat)	Leaf habit	Plant growth form	Twig cross-sectional area (mm <sup>2</sup> )	Total leaf area per twig (mm <sup>2</sup> )
	Rubiaceae	<i>Gardenia jasminoides</i> (4)	BE	Shrubs	5.92 ± 0.32	190.30 ± 68.69
	Staphyleaceae	<i>Euscaphis japonica</i> (1)	BD	Shrubs	13.19	480.12
	Styracaceae	<i>Styrax confuses</i> (10)	BD	Trees	3.27 ± 1.14	115.46 ± 36.45
	Symplocaceae	<i>Symplocos paniculata</i> (1)	BD	Shrubs	6.59	139.12
		<i>Symplocos sumuntia</i> (5)	BE	Shrubs	2.59 ± 0.24	85.64 ± 22.59
		<i>Symplocos setchuensis</i> (10)	BE	Trees	9.92 ± 3.61	177.02 ± 106.64
		<i>Symplocos stellaris</i> (6)	BE	Shrubs	16.07 ± 5.33	236.69 ± 83.73
	Theaceae	<i>Eurya muricata</i> (6)	BE	Shrubs	4.57 ± 0.74	121.86 ± 43.85
		<i>Eurya rubiginosa</i> var. <i>attenuata</i> (3)	BE	Shrubs	5.35 ± 1.47	116.45 ± 24.31
	Ulmaceae	<i>Celtis tetrandra</i> (8)	BD	Trees	7.14 ± 5.42	260.30 ± 56.47
		<i>Zelkova schneideriana</i> (3)	BD	Trees	12.09 ± 2.53	297.17 ± 78.15
Mesophytic	Pinaceae	<i>Pinus massoniana</i> (6)	EC	Trees	10.97 ± 0.81	146.32 ± 86.05
	Aquifoliaceae	<i>Ilex buergeri</i> (1)	BE	Shrubs	2.80	163.52
		<i>Ilex latifolia</i> (3)	BE	Trees	4.18 ± 1.38	187.86 ± 26.54
		<i>Ilex purpurea</i> (2)	BE	Trees	5.98 ± 0.33	114.54 ± 18.91
	Corylaceae	<i>Carpinus turczaninowii</i> (4)	BD	Trees	2.28 ± 0.10	164.88 ± 52.21
	Daphniphyllaceae	<i>Daphniphyllum macropodum</i> (6)	BE	Trees	11.30 ± 2.97	323.31 ± 48.99
	Ebenaceae	<i>Diospyros kaki</i> var. <i>silvestris</i> (4)	BD	Trees	8.92 ± 6.16	283.70 ± 217.26
	Elaeocarpaceae	<i>Elacocarpus japonicus</i> (2)	BD	Trees	2.70 ± 1.10	114.55 ± 66.67
	Ericaceae	<i>Rhododendron mariesii</i> (1)	BD	Shrubs	1.81	84.06
		<i>Rhododendron ovatum</i> (22)	BE	Shrubs	1.56 ± 0.28	91.53 ± 31.28
		<i>Vaccinium mandarinorum</i> (1)	BD	Shrubs	1.59	77.44
		<i>Vaccinium bracteatum</i> (4)	BE	Shrubs	3.28 ± 1.36	134.85 ± 93.54
	Fagaceae	<i>Castanea seguinii</i> (5)	BD	Trees	5.15 ± 1.06	283.80 ± 52.71
		<i>Castanopsis carlesii</i> (33)	BE	Trees	2.31 ± 0.99	189.67 ± 71.76
		<i>Castanopsis fargesii</i> (27)	BE	Trees	3.11 ± 1.34	119.94 ± 58.10
		<i>Castanopsis sclerophylla</i> (22)	BE	Trees	6.24 ± 2.36	205.14 ± 65.95
		<i>Cyclobalanopsis gilva</i> (15)	BE	Trees	3.37 ± 1.14	150.80 ± 62.13
		<i>Cyclobalanopsis glauca</i> (11)	BE	Trees	4.69 ± 1.37	164.66 ± 49.79
		<i>Cyclobalanopsis myrsinaefolia</i> (15)	BE	Trees	3.14 ± 1.11	124.09 ± 41.40
		<i>Cyclobalanopsis nubium</i> (14)	BE	Trees	7.54 ± 4.07	208.83 ± 48.26
		<i>Cyclobalanopsis stewardiana</i> (13)	BE	Trees	4.96 ± 2.17	201.94 ± 71.32
		<i>Lithocarpus henryi</i> (2)	BE	Trees	8.36 ± 1.82	373.69 ± 34.25
		<i>Lithocarpus glaber</i> (29)	BE	Trees	4.79 ± 1.94	156.26 ± 57.45
		<i>Quercus acutissima</i> (5)	BD	Trees	10.39 ± 4.55	324.72 ± 203.79
		<i>Quercus fabri</i> (5)	BD	Trees	6.42 ± 1.33	406.11 ± 210.95
	Hamamelidaceae	<i>Distylium myricoides</i> (12)	BE	Trees	3.49 ± 0.98	141.80 ± 44.49
		<i>Liquidambar formosana</i> (2)	BE	Trees	9.34 ± 1.59	351.21 ± 146.82
		<i>Loropetalum chinense</i> (14)	BE	Shrubs	1.56 ± 0.59	81.59 ± 38.40
	Lauraceae	<i>Cinnamomum camphora</i> (3)	BE	Trees	7.85 ± 2.84	242.74 ± 52.44
		<i>Litsea coreana</i> var. <i>sinensis</i> (1)	BE	Trees	4.66	104.78
		<i>Litsea cubeba</i> (7)	BD	Shrubs	6.61 ± 2.79	271.37 ± 46.86
		<i>Machilus thunbergii</i> (16)	BE	Trees	6.83 ± 2.65	213.31 ± 116.25
		<i>Neolitsea aurata</i> (13)	BE	Trees	3.48 ± 1.31	168.51 ± 51.00
		<i>Sassafras tzumu</i> (9)	BD	Trees	17.72 ± 8.71	585.26 ± 282.78
	Leguminosae	<i>Dalbergia hupeana</i> (3)	BD	Trees	10.60 ± 1.83	497.37 ± 97.38
		<i>Dalbergia millettii</i> (2)	BD	Shrubs	3.52 ± 0.95	125.54 ± 55.90
		<i>Ormosia henryi</i> (1)	BE	Trees	18.35	431.88
	Meliaceae	<i>Melia azedarach</i> (1)	BE	Trees	8.22	227.14
	Moraceae	<i>Ficus erecta</i> var. <i>beeheyana</i> (1)	BD	Shrubs	9.32	184.74
	Myricaceae	<i>Myrica rubra</i> (23)	BE	Trees	7.15 ± 2.40	235.53 ± 86.76
	Myrtaceae	<i>Syzygium buxifolium</i> (10)	BE	Shrubs	2.34 ± 1.35	67.68 ± 19.93
	Oleaceae	<i>Osmanthus cooperi</i> (1)	BE	Shrubs	3.14	164.27
	Proteaceae	<i>Helicia cochinchinensis</i> (1)	BE	Shrubs	3.15	170.97
	Rhamnaceae	<i>Rhamnus utilis</i> (1)	BD	Shrubs	5.76	256.64
	Rosaceae	<i>Photinia serrulata</i> (1)	BE	Trees	2.89	228.98
		<i>Photinia glabra</i> (4)	BE	Shrubs	4.41 ± 1.04	217.61 ± 25.19
		<i>Raphiolepis indica</i> (1)	BE	Shrubs	3.24	81.46
	Rubiaceae	<i>Gardenia jasminoides</i> (1)	BE	Shrubs	4.86	327.29
		<i>Randia cochinchinensis</i> (2)	BE	Shrubs	3.99 ± 0.45	187.82 ± 30.26
	Symplocaceae	<i>Symplocos anomala</i> (5)	BE	Trees	1.34 ± 0.21	74.35 ± 21.07
		<i>Symplocos heishanensis</i> (3)	BE	Trees	2.28 ± 0.19	82.50 ± 18.70
		<i>Symplocos lancifolia</i> (4)	BE	Shrubs	2.66 ± 1.24	134.75 ± 63.95
		<i>Symplocos setchuensis</i> (8)	BE	Trees	6.86 ± 4.27	201.73 ± 88.55
		<i>Symplocos stellaris</i> (18)	BE	Shrubs	17.13 ± 8.15	258.92 ± 114.21
		<i>Symplocos sumuntia</i> (25)	BE	Shrubs	2.07 ± 0.67	87.57 ± 51.54
	Styracaceae	<i>Styrax confuses</i> (2)	BD	Trees	3.51 ± 1.48	102.73 ± 0.16
		<i>Styrax japonicus</i> (1)	BD	Shrubs	10.56	205.86
	Theaceae	<i>Camellia fraterna</i> (18)	BE	Shrubs	1.27 ± 0.32	70.14 ± 30.85
		<i>Cleyera japonica</i> (6)	BE	Trees	4.42 ± 1.28	148.94 ± 53.75
		<i>Eurya muricata</i> (10)	BE	Shrubs	3.88 ± 0.69	111.33 ± 19.53
		<i>Eurya nitida</i> (4)	BE	Shrubs	2.58 ± 1.06	99.13 ± 36.89
		<i>Eurya rubiginosa</i> var. <i>attenuata</i> (15)	BE	Shrubs	4.04 ± 1.27	137.48 ± 47.84

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Table A1 (continued)

Habitat	Taxonomic family	Species (number of individuals sampled per species in all plots in each habitat)	Leaf habit	Plant growth form	Twig cross-sectional area (mm <sup>2</sup> )	Total leaf area per twig (mm <sup>2</sup> )
Wet		<i>Schima superba</i> (54)	BE	Trees	12.38 ± 4.07	250.19 ± 80.14
		<i>Ternstroemia gymnanthera</i> (1)	BE	Trees	5.96	84.84
	Anacardiaceae	<i>Choerospondias axillaris</i> (3)	BD	Trees	16.06 ± 3.65	853.20 ± 320.78
	Aquifoliaceae	<i>Ilex cornuta</i> (4)	BE	Shrubs	5.89 ± 1.54	238.31 ± 54.23
		<i>Ilex kengii</i> (1)	BE	Shrubs	2.2	126.64
		<i>Ilex purpurea</i> (2)	BE	Trees	2.29 ± 0.82	159.76 ± 50.40
	Bursereaceae	<i>Canarium album</i> (2)	BE	Trees	3.68 ± 0.58	140.20 ± 38.80
	Corylaceae	<i>Carpinus turczaninowii</i> (3)	BD	Trees	2.80 ± 0.38	121.96 ± 36.54
	Daphniphyllaceae	<i>Daphniphyllum macropodum</i> (7)	BE	Trees	9.51 ± 3.08	244.07 ± 99.58
	Ebenaceae	<i>Diospyros tsangii</i> (1)	BD	Shrubs	4.3	156.29
	Elaeocarpaceae	<i>Elaeocarpus decipiens</i> (3)	BE	Trees	9.05 ± 1.46	601.56 ± 224.18
		<i>Elacocarpus japonicus</i> (7)	BD	Trees	2.69 ± 0.63	136.99 ± 55.12
	Ericaceae	<i>Vaccinium trichocladum</i> (1)	BE	Shrubs	13.82	292.71
	Fagaceae	<i>Castanopsis carlesii</i> (1)	BE	Trees	1.46	354.43
		<i>Castanopsis fargesii</i> (18)	BE	Trees	4.38 ± 2.35	134.89 ± 41.75
		<i>Cyclobalanopsis gilva</i> (5)	BE	Trees	4.30 ± 1.27	180.84 ± 52.87
		<i>Cyclobalanopsis myrsinaefolia</i> (3)	BE	Trees	2.93 ± 0.57	170.28 ± 77.45
		<i>Cyclobalanopsis stewardiana</i> (1)	BE	Trees	3.24	78.54
		<i>Lithocarpus glaber</i> (1)	BE	Trees	6.32	138.16
		<i>Lithocarpus henryi</i> (5)	BE	Trees	6.25 ± 1.54	245.26 ± 67.91
	Hamamelidaceae	<i>Liquidambar formosana</i> (3)	BD	Trees	6.40 ± 0.69	289.60 ± 73.65
	Illiciaceae	<i>Illicium lanceolatum</i> (3)	BE	Trees	6.52 ± 0.90	235.91 ± 8.70
	Lauraceae	<i>Cinnamomum japonicum</i> (3)	BE	Trees	3.12 ± 0.18	134.80 ± 66.91
		<i>Machilus leptophylla</i> (5)	BE	Trees	17.61 ± 8.66	533.85 ± 152.59
		<i>Machilus thunbergii</i> (9)	BE	Trees	6.54 ± 2.43	228.49 ± 100.52
		<i>Neolitsea aurata</i> (9)	BE	Trees	3.71 ± 1.07	172.25 ± 103.16
		<i>Phoebe sheareri</i> (6)	BE	Shrubs	8.44 ± 1.84	245.17 ± 112.41
	Moraceae	<i>Ficus erecta</i> var. <i>beecheana</i> (3)	BD	Shrubs	7.97 ± 2.15	289.46 ± 111.85
	Oleaceae	<i>Osmanthus cooperi</i> (1)	BE	Shrubs	3.49	127.25
	Proteaceae	<i>Helicia cochinchinensis</i> (6)	BE	Shrubs	3.59 ± 1.41	138.97 ± 28.28
	Rhamnaceae	<i>Hovenia dulcis</i> (1)	BD	Trees	12.78	418.17
	Rosaceae	<i>Photinia glabra</i> (1)	BE	Shrubs	2.01	90.64
	Rubiaceae	<i>Lasianthus lancilimbus</i> (5)	BE	Shrubs	3.98 ± 2.22	154.45 ± 29.82
	Sabiaceae	<i>Meliosma rigida</i> (1)	BE	Shrubs	7.28	278.88
	Styracaceae	<i>Alniphyllum fortunei</i> (1)	BD	Trees	7.21	561.06
		<i>Styrax suberfolius</i> (2)	BE	Trees	3.22 ± 0.37	188.31 ± 25.80
	Symplocaceae	<i>Symplocos anomala</i> (7)	BE	Trees	1.65 ± 0.41	112.17 ± 40.66
		<i>Symplocos glauca</i> (7)	BE	Shrubs	9.08 ± 2.12	268.38 ± 80.07
		<i>Symplocos laurina</i> (4)	BE	Shrubs	5.91 ± 1.78	278.44 ± 112.96
		<i>Symplocos stellaris</i> (3)	BE	Shrubs	14.95 ± 3.90	179.60 ± 30.10
		<i>Symplocos sumuntia</i> (3)	BE	Shrubs	2.84 ± 0.91	119.64 ± 5.91
	Theaceae	<i>Camellia fraterna</i> (9)	BE	Shrubs	1.38 ± 0.45	119.05 ± 88.66
		<i>Camellia oleifera</i> (2)	BE	Shrubs	6.25 ± 0.78	261.53 ± 33.86
		<i>Cleyera japonica</i> (2)	BE	Trees	4.70 ± 1.64	140.51 ± 46.20
		<i>Eurya japonica</i> (1)	BE	Shrubs	1.43	58.07
		<i>Eurya loquaiana</i> (4)	BE	Shrubs	2.00 ± 0.70	122.64 ± 85.92
		<i>Eurya muricata</i> (7)	BE	Shrubs	3.61 ± 0.62	84.49 ± 12.90
		<i>Eurya nitida</i> (5)	BE	Shrubs	1.56 ± 0.52	104.52 ± 68.24
		<i>Eurya rubiginosa</i> var. <i>attenuata</i> (5)	BE	Shrubs	2.31 ± 0.30	195.72 ± 182.95
		<i>Schima superba</i> (4)	BE	Trees	12.44 ± 4.31	231.43 ± 31.23
Ulmaceae	<i>Aphananthe aspera</i> (2)	BD	Trees	3.15 ± 0.80	231.87 ± 22.93	
Verbenaceae	<i>Clerodendrum cyrtophyllum</i> (1)	BD	Shrubs	13.79	335.12	

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