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Original article

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

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A B S T R A C T

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.

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; McGlinn 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