The relationship between trunk- and twigwood density shifts with tree size and species stature

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ABSTRACT

The functional significance of wood density in tree species is widely recognized but the relationship between trunk- and twigwood density, along with any shifts due to tree size and species stature, are as yet poorly understood. We analyzed paired trunk- and twigwood samples from 674 trees, representing 71 species in a subtropical evergreen forest to fill this knowledge gap. We found that larger tree size (i.e. diameter) results in denser trunkwood but lighter twigwood, whereas species stature affects only trunkwood negatively. Trunk- and twigwood density did not vary consistently with tree size and species stature, suggesting some functional divergence between the two locations. Generally, trunk- and twigwood density scaled positively and isometrically, with trunkwood being on average 8.3% denser than twigwood. However, there was a systematic increase in the relative difference in their densities from 2% to 15% across tree size groups. The relationship between trunk- and twigwood density overall is moderately strong ($R^2 = 0.3$–0.6), but depends on both tree size and stature, becoming weaker for larger size and taller stature groups. Collectively, this study highlights the role of plant size in shaping wood density variation and coordination.

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1. Introduction

Wood density is a key functional trait for ligneous plant species because of its relevance to ecologically important characteristics such as mechanical stability, hydraulic conductance and life history (Bucci et al., 2004; Van Gelder et al., 2006; Poorter et al., 2010; McCulloh et al., 2011). It has been proposed as an integrator of a wood economics spectrum (Chave et al., 2009) and as a pivotal axis of plant functional strategies (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013).

While efforts in documenting and comparing wood density usually focus on wood structures located within tree trunks, there are only a limited number of surveys concerning wood structures of terminal twigs (De Micco et al., 2008; Patiño et al., 2009; Yao et al., 2015). Here we use the term "twigwood" in a narrow sense; it is defined *ad hoc* as small branch terminals with diameter < 2 cm but without current-year shootings (Patiño et al., 2009; Sarmiento et al., 2011). Twigwood supports foliar systems and provides hydraulic paths to maintain photosynthesis and transpiration.

Because it forms a large volume of the tree canopy, twigwood, like branchwood in a broader sense, can constitute an appreciable proportion of tree biomass (Adam et al., 1993; Hilton, 2001). More importantly, compared with trunkwood, twigwood has contrasting anatomic properties (Fegel, 1941; Manwiller, 1974; Bhat et al., 1989; Douglas and Floyd, 1994) and can deliver distinctive biomechanical and hydraulic functions (Yang and Tyree, 1993; Domec and Gartner, 2002; De Micco et al., 2008; Gurau et al., 2008; Schuldt et al., 2013). For example, twigwood has a reduced proportion of vessel lumen area, increased resistance to embolism and decreased safety margin to sustain critical buckling load. Since wood density in general is a good indicator of tree mechanics and hydraulics, twigwood density (ρ_{twig}) may also be considered an ecologically important trait (Patiño et al., 2009); but its variation and correlates are only just beginning to be explored (e.g. Patiño et al., 2009; Sarmiento et al., 2011; Schuldt et al., 2013).

One of the core questions in plant functional ecology is how wood density co-varies with other ecologically important traits (Van Gelder et al., 2006; Baraloto et al., 2010). For example, trunkwood density (ρ_{trunk}) has been shown to depend upon both tree size (McKinley et al., 2000; Githiomi and Kariuki, 2010; Deng et al., 2014) and species' stature (i.e. asymptotic height of adults, Woodcock and Shier, 2003; Falster and Westoby, 2005; Van

Gelder et al., 2006). We sought to test whether similar relationships can be demonstrated for twigwood density (ρ_{twig}), because this would demonstrate a functional coordination or divergence at the two locations. Given the common genetic regulation and biophysical coordination within individual trees, ρ_{twig} and ρ_{trunk} should be positively related (Sarmiento et al., 2011) and they are thus expected to covary consistently with tree size and species stature. However, because twigs and trunks are subject to different ontogenetic, mechanic and hydraulic constraints (Niklas, 1997; Domec and Gartner, 2002), ρ_{twig} and ρ_{trunk} could have contrasting relationships with tree size and/or species stature. Furthermore, the strength of ρ_{twig}–ρ_{trunk} relationship could shift with tree size and species stature because organs of small-sized plants generally exhibit less within-individual variation in their physiological and structural roles (Kramer and Kozlowski, 2012). As a result we predicted that there would be larger differences and weaker correlations between ρ_{trunk} and ρ_{twig} for larger trees and taller statured species.

Here we analyzed trunk- and twigwood density for 674 paired samples from 71 subtropical forest tree species with a wide range of habitat preferences and life histories. The main objective is to evaluate the relationship between trunk- and twigwood density, along with any shifts due to tree size and species stature.

2. Materials and methods

2.1. Study site and species

Field data for this study was collected from the Heishiding Natural Reserve (N23°27′, E111°52′), Guangdong province, southern China. The Reserve covers ca. 4200 ha of low, hilly terrain varying between 150 and 1000 m above sea level, supporting large areas of well-preserved forest and bushland. The average annual temperature and precipitation are 19.6 °C and 1740 mm respectively, with most of the rain occurring in summer (June–August). Evergreen broadleaf forests dominated by the families Lauraceae, Theaceae, Magnoliceae, Fagaceae, Hamamelidaceae and Elaeocarpaceae are widespread within the Reserve. The most common canopy species are *Altingia chinensis* (Hamamelidaceae), *Castanopsis carlesii* (Fagaceae), *Artocarpus styracifolius* (Moraceae) while subcanopy layers are dominated by *Cryptocarya concinna* (Lauraceae) and *Neolitsea phanerophlebia* (Lauraceae).

In the interior of Heishiding Natural Reserve, a contiguous forest stand of about 50 ha was surveyed. The average canopy height of the surveyed area was estimated to be about 25 m. Considering only trunks with diameter at breast height (d.b.h.) >5 cm, the mean d.b.h. was 13 ± 10 cm (mean ± standard error) and the mean stand density of was 1540 stems/ha. We selected 71 widespread evergreen broadleaf species (see Appendix 1), representing 30 families and 46 genera to determine wood density. Species of Fagaceae (12 species) and Lauraceae (9 species) were the most widely represented in our dataset. The life form and maximum height for each of our species are available in Flora Republicae Popularis Sinicae (English and Chinese language versions available online at http://foc.eflora.cn) and Atlas of China's Higher Plants (http://pe.ibcas.ac.cn/tujian/tjsearch.aspx). The stature range across all 71 species is 5–35 m and averages 15 m. Based on field experience, these species occupy a diversity of habitat types including ridges and valleys, gaps and closed understories.

2.2. Wood sampling and density determination

All data were collected during September through November (after the growing season) in 2014. Wood density data were collected from a total of 674 trees, comprising samples from 5 to 20 randomly placed individuals for each species. Diameter at breast height (d.b.h.) of all trees was recorded at the time of sampling (range 5–45 cm). For each individual, trunkwood was sampled using a borer, while twigwood was sampled by harvesting suitably sized branch terminals. For each tree a trunkwood core about 3–5 cm long was extracted at a height of 1.3 m using a tree borer with 0.5 cm caliber, and a segment of twig at the canopy fringe was truncated using a tree pruner. We took care to sample twigs with diameter < 1 cm at a distance ca. 30–50 cm back from the branch tips and without the current-year shootings. All wood samples were wrapped with moist filter paper for transport to the laboratory. After removing bark material, twigwood was trimmed to approximate a cylindrical shape (mean dimensions ± 1 S.D.: 4.67 ± 0.49 cm in length, 0.48 ± 0.05 cm in diameter). Branch knots were deliberately avoided. Wood cores were also truncated at two ends so as to approximate a cylinder. The diameter at both ends and the length of well-trimmed cores and twig segments were measured using a vernier caliper to the nearest 0.01 mm. Green volume was approximated using measured dimensions under an assumption of a circular cross-sectional area. Wood dry mass was weighed to the nearest 0.0001 g after 72-h oven treatment at 80 °C. All these procedures were executed according to the protocol of Osazuwa-Peters and Zanne (2011).

We verified that ρ_{twig} and diameter of twig segments of samples were not correlated ($r = 0.027$, $P = 0.5$, $n = 674$), thereby warranting comparable ρ_{twig} estimation within a limited range of twig size and/or age. As wood cores of 3–5 cm length in small-d.b.h. trunks can include tree pith and thus underestimate wood density compared with large-d.b.h. trunks, we regressed ρ_{trunk} against the ratio of core length to trunk d.b.h. as an objective means to estimate any bias in wood cores toward including pith. While a decreasing trend in wood density toward piths was evident ($k = -0.054$, $P = 0.013$, $n = 674$), the R^2 was only 0.008. As a result we chose to use raw ρ_{trunk} values without removing the radial trend.

2.3. Statistical analyses

To test the hypothesis that twigwood and trunk wood co-vary consistently with size and stature we used a range of regression and statistical tests. Linear mixed-effects models were built to evaluate the effects of tree size and species stature on wood density:

$$\rho_{ij} = \beta_0 + \beta_1 dbh_{ij} + \beta_2 H_{\max_i} + \mu_i + \varepsilon_{ij}$$

where ρ_{ij} is the wood density of the jth individual tree of the ith species; dbh_{ij} and $H_{\max i}$ are tree size (i.e. diameter) and species stature, respectively, with β_1 and β_2 being their corresponding fixed effects. β_0 is the fixed intercept, and μ_i is the random effect incorporated by species. Tree size (i.e., d.b.h.) and species stature were log-transformed before use as explanatory variables, with separate models fitted to ρ_{trunk}, ρ_{twig} and their relative differences ($R_{\Delta\rho}$), calculated as:

$$R_{\Delta\rho} = (\rho_{trunk} - \rho_{twig})/\rho_{twig}$$

Linear mixed-effects models were estimated using restricted maximum likelihood (REML). Marginal and conditional R^2 (the variation explained by fixed and random effects, respectively) of linear mixed-effects models were calculated following the method described by Nakagawa and Schielzeth (2013).

Paired t-tests were used to test whether the difference ($\Delta\rho$) between ρ_{trunk} and ρ_{twig} exceeded zero (one-tail test). The bivariate relationship between ρ_{trunk} and ρ_{twig} was estimated as below using standard major axis regression:

$$\log(\rho_{trunk}) = \log(\alpha) + \beta\log(\rho_{twig})$$