Andrés González-Melo

Radial variations in wood density, and their implications for above-ground biomass estimations, in a tropical high-andean forest

Abstract: Wood density (WD) is a central trait to explain tree functioning, and is also an important predictor of tree above-ground biomass (AGB). Therefore, radial trends in WD (i.e., from pith to bark) may have important implications in understanding tree life-history variations, as well as in forest biomass and carbon estimations. The occurrence of these radial trends in WD is thought to vary among forests, particularly with canopy openness and stratification. Yet, most of the studies on this topic in tropical forests have been conducted on lowland closed-canopy forests, while very little is known about the prevalence and magnitude of these trends among trees from open-canopy forests, such as high-mountain forests.
I examined radial gradients in WD and explored their implications for AGB estimations.
Radial wood cores were taken with increment borers from 69 trees belonging to 18 species from a high-Andean forest. Each wood core was cut every 1-cm, and WD was measured for every 1-cm segment. Errors in AGB estimations that resulted from not considering radial trends in WD were estimated for each tree and species.
Eight out of eighteen species had significant radial trends in WD. Among these species, two species showed decreases of WD towards the bark, one species showed increments of WD from pith to bark, and five species showed U-shaped gradients (i.e., high WD near the pith and bark, and relatively low WD at intermediate diameters). The prevalence of U-shaped radial trends in WD may be related to the relatively open and less stratified canopy of the study forest. Not taking into account radial trends in WD led in general to under-estimations of AGB (averaging $-7.66\,\%$ when using mean WD, and $-5.56\,\%$ for outer WD) in most of the study species, suggesting that tropical high-Andean forests may possibly store more biomass carbon than has been previously estimated.
These findings are important to expand our knowledge on wood allocation patterns during tree ontogeny, and also to improve the accuracy of biomass and carbon estimations in tropical high-Andean forests.

Keywords: wood density, above-ground biomass, radial variations, tropical high-Andean trees

Adresses: A.G. Melo, Biology Department, Faculty of Natural Sciences, Universidad del Rosario, Carrera 24 # 63C-69, Bogotá, Colombia, e-mail: germana.gonzalez@urosario.edu.co;
ⓘ https://orcid.org/0000-0003-0069-456X

Introduction

Wood density (WD, g cm^{-3})is a commonly measured plant trait (e.g., Chave et al., 2009), and is considered a central trait to understand tree functioning and performance (e.g., Chave et al., 2009; Visser et al., 2016). For instance, WD is generally related to wood hydraulic (Santiago et al., 2004, 2019) or mechanical properties (King et al., 2006); and has been suggested to balance a trade-off between stem construction and maintenance costs, with low-WD species achieving needed stem strength at a lower construction cost (e.g., Anten & Shieving, 2010), and high-WD species having lower stem maintenance costs (Larjavaara & Muller-Landau, 2010). Furthermore, WD also plays a key role in forest biomass and carbon estimations, as it is usually the second most important predictor, after stem size, of above-ground biomass (Chave et al., 2014).

It is well established that WD can vary substantially along environmental gradients (Wiemann & Williamson, 2002; Ter Steege et al., 2006). For example, a number of studies have shown that WD tends to decrease with soil fertility (e.g., Muller-Landau, 2004; Ter Steege et al., 2006; Fortunel et al., 2013) or with mean annual precipitation (e.g., Wiemann & Williamson, 2002; Chave et al., 2009; Martínez-Cabrera et al., 2009). Moreover, the literature indicates that WD varies considerably across species (e.g., Muller-Landau, 2004, Chave et al., 2009). In particular, WD is related to successional position and then reflects a slow-fast continuum in plant performance, where slow-growing species typically have dense wood (Muller-Landau, 2004; Chave et al., 2009; Plourde et al., 2015).

Wood density can also vary radially within stems (i.e., from pith to bark) during tree ontogeny (e.g., Williamson & Wiemann, 2010a; Lachenbruch et al., 2011). Yet, in biomass estimation studies, these radial changes in WD have received much less attention in comparison to interspecific or environmental variation of WD. In general, there are three main patterns of radial variations in WD. Positive patterns (i.e., increments of WD towards the bark) that are typical of fast-growing species (Wiemann & Williamson, 1989; Williamson & Wiemann, 2010a), negative ones (i.e., decreases of WD) that tend to be common among slow-growing species (Hietz et al., 2013; Plourde et al., 2015), and U-shaped patters in which wood is dense near the pith and bark, but light at intermediate stem diameters (Williamson et al., 2012; Osazuwa-Peters et al., 2014).

Different factors, that are not mutually exclusive, may explain the occurrence of these radial changes in WD. First, the age of the vascular cambium that can influence the size of wood cells (Lachenbruch et al., 2011; Williamson & Wiemann, 2010a). Second, the deposition of wood extractives, in heartwood or sapwood, that can affect WD via increments in wood mass (Lehnbach et al., 2019). Third, the size of stems because trees can adjust their wood in response to changes in mechanical, storage and hydraulic demands during ontogeny (Nock et al., 2009; Rungwattana & Hietz, 2017). In addition, a number of studies have suggested that radial trends in WD may reflect, to some extent, the temporal and spatial shifts in light availability that trees experience as they grow (e.g., Woodcock & Shier, 2002; Williamson & Wiemann, 2010a; Hietz et al., 2013; Osazuwa et al., 2014). For instance, juveniles of light-demanding species typically produce light wood to favor fast growth in gap openings and later, as adults, they tend to produce denser wood, probably to enable crown expansion and increase mechanical stability (Williamson & Wiemann, 2010a; Osazuwa et al., 2014). In contrast, shade-tolerant species generally start producing dense wood which may be advantageous to survive in the shaded understory, and when they reach more favorable canopy layers, they produce lighter wood likely to increase their height and diameter growth (Woodcock & Shier, 2002; Hietz et al., 2013).

If radial shifts in WD are related to both vertical (i.e., from the understory to the canopy) and horizontal (i.e., via gap openings) gradients in light availability (Woodcock & Shier, 2002), then it is likely that these radial shifts in WD vary among forests that differ in terms of canopy openness and stratification (e.g., Wiemann & Williamson, 1989). Yet, evidence supporting this idea is limited, particularly for tropical forest trees (Wiemann & Williamson, 1989), mainly because most studies on this topic in tropical forests have been conducted in lowland and closed-canopy forests (Williamson & Wiemann, 2010a; Hietz et al., 2013; Plourde et al., 2015; Osazuwa-Peters et al., 2014), while very few have been done in more open-canopy forests such as tropical high-Andean forests (but see Wiemann & Williamson, 1989). This limits our understanding of ontogenetic shifts in wood allocation patterns and tree functioning among tropical mountain trees.

Beyond its functional significance (e.g., Chave et al., 2009), WD is also a key predictor of above-ground biomass (AGB; Chave et al., 2014). Some studies on AGB estimations, particularly at larger scales, use averaged WD values, at the species, genus or family level (e.g., Zanne et al., 2009); or values from branches or the outer part of the trunk (e.g., Baraloto et al., 2012). However, not taking into account radial trends in WD may lead to biases in AGB estimations (Nock et al., 2009; Schüller et al., 2013; Plourde et al., 2015). For example, the use of WD values from the outer part of the stem may cause over-estimations of AGB in fast-growing species (e.g., Nock et al., 2009),

as in these species WD is typically higher in outer than in inner wood (e.g., Williamson & Wiemann, 2010a), while the opposite trend (i.e., under-estimations in AGB) would be expected for slow-growing species (e.g., Schüller et al., 2013).

High-Andean forests of central Colombia are part of the Tropical Andes Biodiversity Hotspot, which is considered a global center of endemism and biodiversity (Myers et al., 2000; Mittermier et al., 2003). These forests also play a central role in the provision of ecosystem services such as carbon storing and water regulation (Armenteras et al., 2003; Torres et al., 2012). However, despite the relevance of these forests, several aspects of their ecology and functioning are still poorly understood. The aim of this study is to increase our understanding of ontogenetic trends in wood and biomass allocations across 18 tree species, with contrasting shade-tolerance, from a tropical high-Andean forest. In particular, I wanted to answer the following questions: (i) How does WD change with stem diameter? and (ii) How do radial changes in WD affect above-ground biomass estimations?

Methods

Study site

The study was conducted in a high-Andean forest located in Guasca (04°51'N, 73°41'W), central Colombia, at 2950 m of elevation. The rainfall pattern in the region is unimodal with a distinct rainy season peaking in July. Mean annual temperature is 13°C and rainfall averages 1714 mm per year (Cantillo et al., 2004). Floristic composition of canopy trees is similar to other nearby high-Andean forests (Cantillo et al., 2004; Avella et al., 2014), and dominant families in the canopy include Clusiaceae, Cunoniaceae, Chrysobalanaceae and Myrsinaceae (personal observation.). The forest was subjected to selective logging of valuable timber species (i.e., Lauraceae spp.) 40–50 years ago. However, based on forest structure and floristic composition, the forest is considered mature.

Species selection and sampling

Eighteen of the most abundant tree species in the canopy and subcanopy were randomly selected, and classified as light-demanding, long-lived light-demanding, or shade-tolerants based on their regeneration light requirements (Mahecha et al., 2012). To measure wood density, core samples were taken to the center of the stem and at breast height (1.3 m), using a 12-mm increment borer (Williamson & Wiemann, 2010b). One core sample was obtained per individual, in three to five individuals per species, for a total of 69 trees. Whenever possible, trees without visible injuries or leaning stems were sampled, as these factors could affect WD measures. Core samples were stored in sealed plastic tubes and placed in a refrigerator until processing in the laboratory (Hietz et al., 2013).

WD measurements

After removing the pith and/or bark, when present, cores were divided into 1-cm segments. For each of these segments, radial position with respect to the inner part of the core, fresh volume, and dry mass were measured. Fresh volume was calculated by the water displacement method and dry mass was obtained after drying the wood segments at 103°C for 24–72 h until constant weight. Wood density per segment was defined as dry mass over fresh volume (Williamson & Wiemann, 2012a). Three different values of WD for each tree were calculated. First, weighted WD (WD_W), which corresponded to the average of all WD values of the 1-cm segments per core, weighted by the stem cross-sectional area that each 1-cm segment represents, and assuming a cylindrical stem (Muller-Landau, 2004). Second, mean WD (WD_M), which is the average of all radial WD values per core. Finally, outer WD (WD_O), that is the mean of WD values from the outer 3 cm of each core. Here, WD_W represents the most accurate estimation of tree WD, for a given stem diameter, than WD_O or WD_M, because it takes into account that outer wood segments contribute more to the whole WD of each tree.

Averaged WD_W, WD_M, and WD_O values were calculated for each species.

Biomass estimations

Above-ground biomass (AGB) was calculated for each tree and species using a general allometric model for tropical humid forests (Chave et al., 2014) as: AGB = exp ($-1.803 - 0.9769 \times E + 0.9769 \times$ log (WD) $+ 2.6739 \times$ log (DBH) $- 0.0299 \times$ log $(DBH)^2$, where DBH is given in cm and E is a parameter depending on climate. For each tree, three values of AGB were calculated: mean AGB (AGB_M), outer AGB (AGB_O), and weighted AGB (AGB_W); using WD_M, WD_O and WD_W values, respectively (Table 2). Then, averaged species values of AGB_W, AGB_M and AGB_O were calculated. Finally, percentage errors in AGB estimations per species were calculated by comparing AGB_O and AGB_M with AGB_W, as follows:

$$\% \text{ error AGB} = ((AGB - AGB_W) \times 100) / AGB_W \quad (\text{Eq. 1})$$

where AGB is AGB_O or AGB_M.

Statistical analyses

Radial trends in WD were examined using linear and generalized models predicting WD based on radial distance. As non-homogeneous gradients in WD have been reported for tropical trees (e.g., Williamson and Wiemann, 2010a; Osazuwa-Peters et al., 2014), I fitted linear and non-linear models (i.e., quadratic and cubic) for each species, and compared these models based on Akaike's Information Criterion corrected for small sample sizes (AIC_C). Lower AIC_C scores indicated a better fit to the data (Burnham & Anderson, 2002). Then, I examined residual plots to confirm linear or non-linear trends. The possible differences between WD_M, WD_O and WD_W, as well as between AGB_W, AGB_M and AGB_O, were evaluated using paired Student's t-tests. All statistical analyses were conducted in the software R 3.2.2 (R Development Core Team, 2016).

Results

Radial variation in WD

Eight out of eighteen species had significant radial trends in WD (44.4%; Table 2, Fig. 1). Among these species, radial changes in WD were best fitted by linear models in three species (16.6%, Table 2). Two of these species (i.e., *Ocotea sericea* and *Podocarpus oleifolius*) are shade-tolerants and had negative gradients in WD (e.g., WD decreased towards the bark), while one species (i.e., *Axinea macrophylla*) is light-demanding and had a positive gradient in WD (i.e., WD increased from pith to bark). Non-linear models

(i.e., quadratic or cubic equations) best explained radial gradients in WD in five species (27.7%, Table 2), which correspond to long-lived, light-demanding species (Table 1). In these five species, WD tends to follow a U-shaped pattern where WD is higher close to the pith and bark, but relatively low at intermediate stem diameters.

Weighted WD (WD_W) differed significantly from mean WD (WD_M; t: 18.86, p<0.001) and outer WD (WD_O; t: 4.67, p<0.001), whereas WD_M and WD_O did not differ significantly (t: 0.17, p>0.05). The use of WD_M, instead of WD_W, led to under-estimations of AGB (e.g., AGB_M) in most of the species (Table 2, Fig. 2). The percentage error in AGB_M estimations averaged -7.66%, ranging from 2.35% in *Ocotea calophylla* to -11.70 in *Myrsine coriacea* (Table 2). Similarly, the use of WD_O caused under-estimations in AGB for all species, excepting *Hedyosmum parvifolium* (Table 2, Fig. 2). The percentage error in AGB_O estimations varied from 2.25 in *Ocotea calophylla*, to -22.0% in *Ocotea sericea* (Table 2), averaging -5.56%. The percentage errors in AGB_M and AGB_O did not differ significantly from one another (t:0.79, p>0.44). AGB_W differed significantly from AGB_M (t:3.98, p<0.001) and AGB_O (t:4.23, p<0.001), while AGB_M and AGB_O were not significantly different (t: 1.99, p>0.05).

Discusion

Radial trends in WD

Negative radial shifts in WD (i.e., decreases of WD towards the bark) were found in two shade-tolerant species, namely *O. sericea* and *P. oleifolius* (Fig. 1,

Table 1. Study species, family, number of trees sampled (n), mean diameter at breast height (DBH), mean height (H) and ecological guild, based on Mahecha et al. (2012), of 18 tree species from a high-Andean forest

| Species	Code	Family	n	DBH (cm)	H (m)	Ecological guild
Axinea macrophylla	Axi_mac	Melastomataceae	5	29.2	18	Light-demanding
Brunellia acutangula	Bru_acu	Brunelliaceae	5	24.2	13	Light-demanding, long-lived
Clethra repanda	Cle_rep	Clethraceae	3	26.2	16	Light-demanding, long-lived
Clusia multiflora	Clu_mul	Clusiaceae	4	26.4	13	Shade-tolerant
Clusia sp.	Clu_sp	Clusiaceae	3	28.6	15	Shade-tolerant
Drymis granadensis	Dry_gra	Winteraceae	5	30.2	13	Light-demanding, long-lived
Hedyosmum crenatum	Hed_cre	Chloranthaceae	4	26.2	10	Light-demanding, long-lived
Hedyosmum parvifolium	Hed_par	Chloranthaceae	3	25.8	9	Light-demanding, long-lived
Myrsine coriacea	Myr_cor	Primulaceae	3	25.9	11	Shade-tolerant
Ocotea calophylla	Oco_cal	Lauraceae	3	31.0	13	Shade-tolerant
Ocotea sericea	Oco_ser	Lauraceae	3	29.1	12	Shade-tolerant
Podocarpus oleifolius	Pod_ole	Podocarpaceae	5	30.6	13	Shade-tolerant
Prunus buxifolia	Pru_bux	Rosaceae	4	31.1	14	Shade-tolerant
Symplocos mucronata	Sym_muc	Symplocaceae	3	27.2	11	Shade-tolerant
Tibouchina lepidota	Tib_lep	Melastomataceae	4	29.3	9	Light-demanding
Weinmannia auriculata	Wei_aur	Cunoniaceae	6	30.2	15	Light-demanding, long-lived
Weinmannia pinnata	Wei_pin	Cuniniaceae	3	25.1	13	Light-demanding, long-lived
Weinmannia tomentosa	Wei_tom	Cuniniaceae	3	25.3	11	Light-demanding, long lived
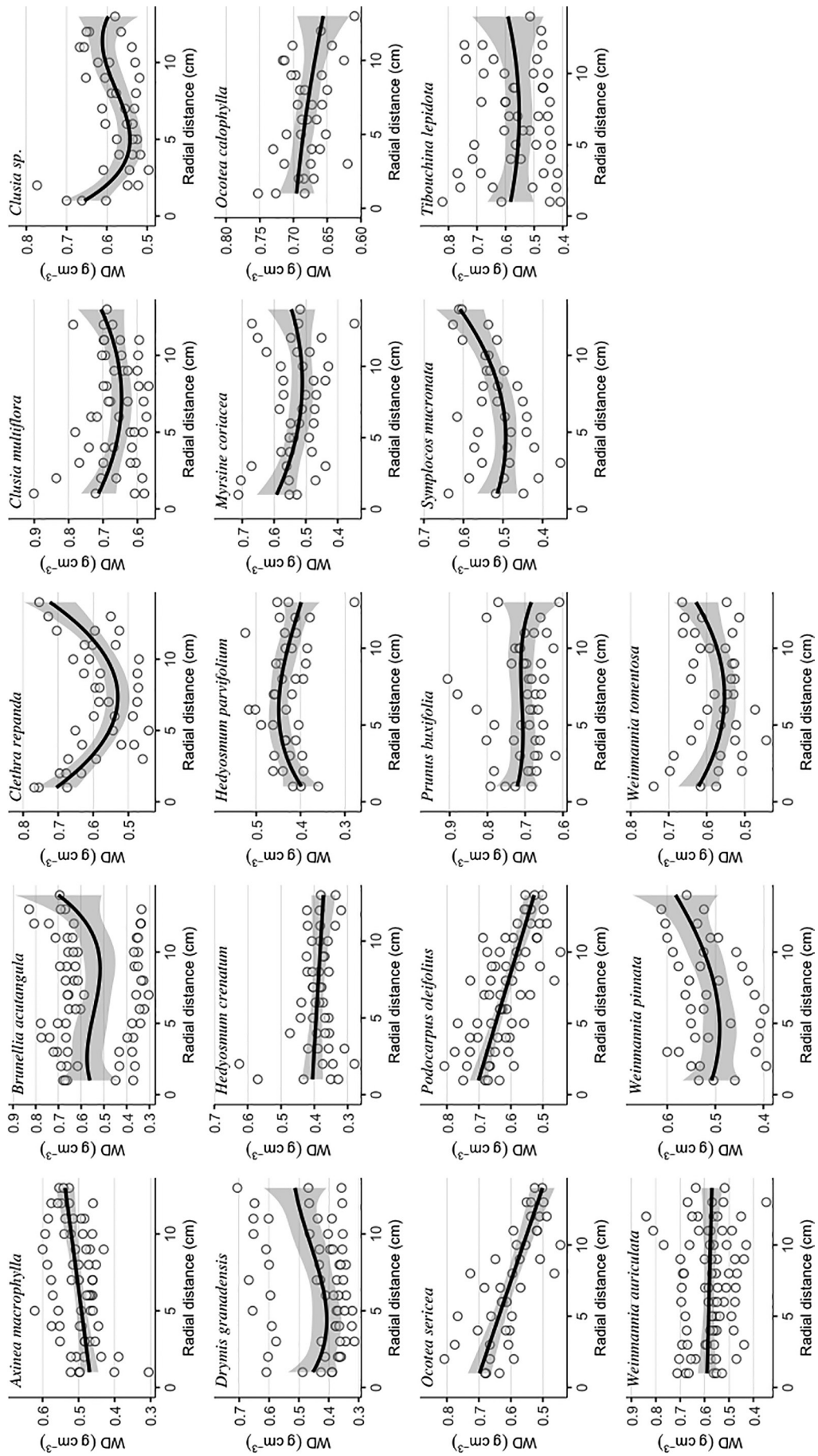
Fig. 1. Radial gradients in WD in 18 tree species from a tropical high-Andean forest. Radial distance refers to the distance from pith to bark. Dots represent individual trees, black lines are best-fit linear or non-linear (i.e., quadratic or cubic, see Table 2) regression models, and gray bands denote standard error

Table 2). There are two possible explanations to the occurrence of negative radial trends in WD in these species. First, these gradients may be the product of the deposition of wood extractives in the inner wood during heartwood formation (Lehnbach et al., 2019), because extractives can increase density via increments in wood mass. This would be the case of *O. sericea*, as heartwood was present in all cores of this species. Since wood extractives are involved in plant defense (e.g., Hillis, 1987), the negative gradient of WD in *O. sericea* may be related to defensive needs. An alternative explanation is that negative gradients in WD reflect the wood allocation strategy of shade-tolerants during ontogeny (e.g., Woodcock & Shier, 2002). For instance, juveniles of shade-tolerant species typically produce dense wood (e.g., Hietz et al., 2013; Plourde et al., 2015), which can limit growth, but may be advantageous to survive in the forest understory because it reduces the risks of pathogen attacks or mechanical damage due to falling branches (e.g., Alvarez-Claire & Kitajima, 2007). Later, when adults have reached more favorable canopy layers, they tend to produce lighter wood probably to favor tree growth (e.g., Woodcock & Shier, 2002). This ontogenetic pattern of WD variation may hold true for *P. oleifolius*, which is a shade-tolerant species representative of old-growth, tropical high-Andean forests.

In contrast, *A. macrophylla*, a light-demanding species, had a positive gradient in WD (i.e., increments from pith to bark; Table 2, Fig. 1). This is in agreement with a number of studies that have reported radial increments of WD in pioneer and light-demanding species (e.g., Woodcock & Shier, 2002; Nock et al., 2009; Hietz et al., 2013; Plourde et al., 2015). Radial increments of WD are thought to provide benefits in terms of growth and mechanical stability (Woodcock & Shier, 2002; Hietz et al., 2013; Bossu et al., 2018). At early ontogenetic stages, light-demanding species may benefit from producing low density wood, because these species tend to regenerate in canopy gaps, and light wood may allow faster growth rates in light environments (e.g., Woodcock & Shier, 2002). Then, as adults, light-demanding species tend to produce dense wood in the outer part of the trunk (Woodcock & Shier, 2002), which may allow them to achieve needed mechanical strength at a lower construction cost than tree species with denser wood (Hietz et al., 2013; Bossu et al., 2018). These benefits in growth and mechanical stability may be at the cost of survival, particularly in juveniles, since low-WD species have higher risks of mechanical or pathogen damage (e.g., Alvarez-Clare & Kitajima, 2007), as well as of hydraulic dysfunction (e.g., Santiago et al., 2018). Another possible, and indirect, cost associated to radial increments of WD is higher stem maintenance costs (i.e., stem respiration), since light-demanding species tend to build thicker stems than shade-tolerant species, and maintenance costs are thought to increase with stem surface area (e.g., Larjavaara & Muller-Landau, 2010).

Non-linear, U-shaped, radial trends were found in five species, all of them corresponding to long-lived, light-demanding species (Table 1, 2; Fig. 1). While U-shaped trends in WD have been reported previously for tropical trees in lowland humid forests

Table 2. Best-fitting models, model parameters, WD values, AGB values, and percentage errors in AGB (mean: % AGBM, outer: % AGBO) for 18 tree species from a tropical high-Andean forest. Significant P-values (<0.05) are shown in bold. See Methods for trait abbreviations

| Species | Models | | | WD | | | AGB | | | | |
	Model	R^2	P	WD_M	WD_O	WD_W	AGB_O	AGB_M	AGB_W	% AGB_M	% AGB_O
Axinea macrophylla	Linear	0.12	**<0.01**	0.50	0.53	0.53	412.3	435.3	431.1	−4.16	1.25
Brunellia acutangula	Cubic	−0.04	>0.05	0.55	0.56	0.60	502.3	519.4	548.1	−9.15	−7.31
Clethra repanda	Quadratic	0.14	**<0.05**	0.59	0.62	0.64	534.2	563.6	580.7	−8.19	−3.19
Clusia multiflora	Quadratic	0.03	>0.05	0.66	0.67	0.72	484.9	491.8	524.1	−7.51	−6.39
Clusia sp.	Cubic	0.03	>0.05	0.58	0.59	0.63	452.5	463.6	490.8	−7.78	−5.61
Drymis granadensis	Cubic	0.08	**<0.05**	0.43	0.47	0.48	323.4	342.9	350.8	−9.22	−5.97
Hedyosmum crenatum	Linear	0.01	>0.05	0.39	0.38	0.45	264.6	263.2	299.4	−11.51	−13.31
Hedyosmum parvifolium	Cubic	0.04	>0.05	0.42	0.43	0.42	383.0	388.9	383.0	0.00	1.5
Myrsine coriacea	Quadratic	0.14	>0.05	0.53	0.52	0.60	646.0	661.2	753.7	−11.7	−13.5
Ocotea calophylla	Quadratic	0.10	>0.05	0.68	0.58	0.72	833.8	0.348	812.0	2.35	2.25
Ocotea sericea	Linear	0.18	**<0.01**	0.60	0.51	0.66	695.9	809.7	896.6	−9.88	−22.0
Podocarpus oleifolius	Linear	0.43	**<0.001**	0.61	0.55	0.67	580.2	513.6	629.4	−7.90	−17.19
Prunus buxifolia	Cubic	0.61	>0.05	0.70	0.69	0.76	496.0	490.6	535.0	−7.47	−7.69
Symplocos mucronata	Quadratic	0.21	**<0.01**	0.51	0.54	0.56	374.5	402.4	410.0	−8.13	−0.97
Tibouchina lepidota	Quadratic	−0.03	>0.05	0.56	0.57	0.61	415.1	426.4	452.8	−8.66	−7.51
Weinmannia auriculata	Linear	−0.01	>0.05	0.58	0.60	0.63	515.2	532.3	561.1	−8.17	−5.24
Weinmannia pinnata	Cubic	0.15	**<0.05**	0.51	0.55	0.56	433.1	476.8	474.9	−8.78	−0.79
Weinmannia tomentosa	Quadratic	0.16	**<0.01**	0.58	0.59	0.63	485.6	497.5	526.6	−7.84	−5.11

(Wiliamson et al., 2012; Osazuwa-Peters et al., 2014), the results of this study suggest that they are also common in tropical high-Andean forests. Yet, a clear understanding of the factors driving these radial trends in WD is still lacking (e.g., Osazuwa-Peters et al., 2014). In comparison to lowland humid forests, tropical high-Andean forests tend to have lower stature, as well as a more open and less stratified canopy (e.g., Asner et al., 2014). As a consequence, I speculate that a large fraction of high-Andean tree species likely regenerates in relatively well-lit environments. In this context, although the species that showed U-shape radial trends in WD start producing wood of intermediate (c. 0.50–0.70) density, they might benefit from the prevailing gap openings by investing in lighter wood at small and intermediate stem diameters. Later, at larger diameters, these species may produce denser wood, either because canopy gaps are closed and light availability is limited, or because they have reached the canopy and need to favor crown expansion and/or increase mechanical stability. Further studies on ontogenetic shifts in light availability and species demographic rates are needed to explain the occurrence of U-shaped radial trends in WD that seem to be common among tropical high-Andean trees.

Density is an integrative property of wood that is influenced, in angiosperms, by the relative abundance and morphology of three cell types: vessels, fibers and parenchyma cells (e.g., Carlquist, 2001). In particular, fibers are thought to be the main drivers of WD variations (e.g., Mártinez-Cabrera et a., 2009; Zieminska et al., 2015), as they are the most abundant cell type and tend to have thicker walls than vessels or parenchyma cells (Zieminska et al., 2013). Therefore, radial variations in WD likely reflect radial shifts in wood anatomy, particularly in fiber fractions and wall thickness (Mc Donald et al., 1995). Yet, a recent study found that the anatomical drivers of radial variations in WD can vary substantially among species (Rungwattana & Hietz, 2017). The extent to which wood anatomical traits explain radial shifts in WD is a subject that merits further study. In addition, it is important to note that in some species, particularly in those without significant radial shifts in WD, conspecific individuals can show divergent ontogenetic trends in WD (Fig. 1). Possibly, differences in growing conditions (i.e., light availability and edaphic factors) among individuals may drive these divergent trends. Future research should consider larger sample sizes, and take into account individual growing conditions, to better understand intraspecific variation in ontogenetic trends in WD.

Radial trends in WD and above-ground biomass estimations

Wood density is, after stem size, the most important predictor of above-ground biomass (AGB; Chave et al., 2014). Then, not taking into account radial trends in WD may led errors in ABG estimations
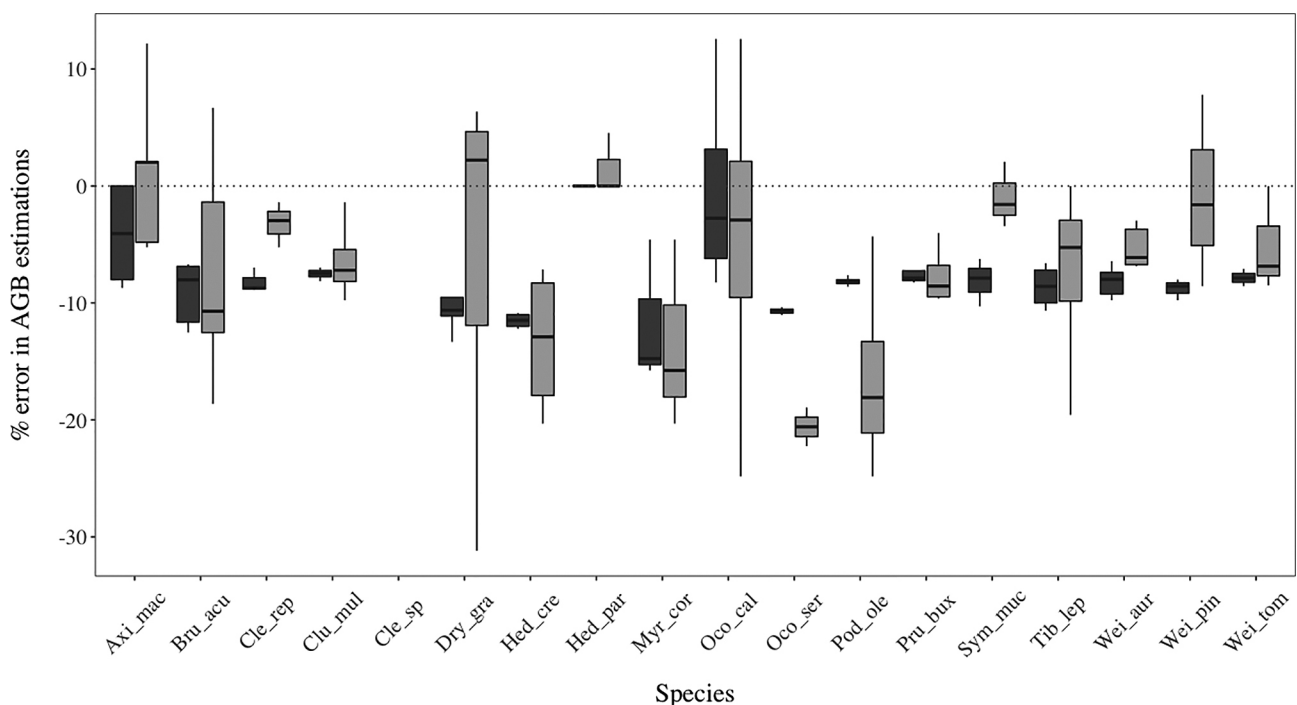

Fig. 2. Percentage errors in AGB estimations for 18 tree species from a tropical high-Andean forest. Black and gray bars represent mean AGB (AGB_M) and outer AGB (AGB_O), respectively. Error bars denote standard deviation. See Table 1 for species codes

(e.g., Schüller et al., 2013; Osazuwa-Peters et al., 2014). The results of this study indicate that not considering radial trends in WD led, in general, to under-estimations of AGB in most of the study species (Fig. 2, Table 2). This indicates that some tropical high-Andean forests may probably have higher AGB (e.g., Álvarez-Davila et al., 2017; Rodríguez-Alarcon et al., 2018; Calbi et al., 2021), and store more biomass carbon, than have been previously estimated. Although forest biomass estimation is increasingly based on remote sensing techniques such as hyperspectral optical imaging and LIDAR (e.g., Réjou-Mechain et al., 2017), it still depends to some degree on field data at the species and stand level (Chave et al., 2014). This suggests that although the averaged percentage errors in AGB estimation found in this study are relatively small ($-7,66$ % using WD_M, and -5.66 % using WD_O), they may lead to misleading interpretations of forest carbon dynamics, if they are uncritically propagated to the stand or regional level.

Furthermore, for most of the studied species, the percentage errors in AGB estimations resulting from using WD_M did not differ considerably from those obtained from using WD_O (Fig. 2). Therefore, instead of using WD_M, WD_O, or averaged WD values from global repositories, a better practice to reduce biases in AGB estimations in these high-Andean forests would be to take wood cores to the center of the stem, and calculate WD for different segments of each core, weighting them by the stem cross sectional area they represent. Yet, this practice may not be feasible for studies that consider a large number of species or individuals. Finally, WD can vary not only radially, but also axially from the base of the stem toward tree top (e.g., Lachenbruch et al., 2011). Then, I suggest that future studies should consider the effects of axial variations in WD on AGB estimations.

Conclusions

This study examined radial variations of WD, and their implications for above-ground biomass (AGB) estimations, in 18 tree species with contrasting shade-tolerance in a tropical high-Andean forest. Significant radial variations in WD were found in eight species. Among these species, one had a positive and linear trend, two showed negative and linear patterns, and five species had U-shaped radial trends. The prevalence of U-shaped radial trends in WD may be related to the relatively open and less stratified canopy of the study forest. Not taking into account radial trends in WD led in general to under-estimations of AGB in most of the study species, suggesting that tropical high-Andean forests may possibly store more biomass carbon than previously assumed.

These insights are important to increase our knowledge on ontogenetic shifts in WD, and then to redefine the functional value of WD among tropical high-Andean tree species. Moreover, the fact that radial trends in WD are common among the study species suggests that interspecific comparisons of WD in high-Andean forests should consider the effect of stem size. The results of this study may also help to reduce uncertainties associated to AGB estimations in high-Andean forests which, in turn, is important to have a better understanding of the role that these forests play on the global carbon cycle and the provision of ecosystem services.

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