



# Wood density is a poor predictor of competitive ability among individuals of the same species



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## ABSTRACT

Competition between immediate neighbors has been regarded as one of the most important forces of natural selection that shapes the species composition, diversity and evolution of plant traits within a community. Here, I examined wood density (WD) variation in populations of two tree species, where individuals have contrasting access to resources. In five *Nothofagus betuloides* and *Nothofagus pumilio* even-aged, mixed second-growth forests in Patagonia (Chile), I sampled pairs of dominant (full access to resources) and the nearest-to-it suppressed individuals (constrained access to resources), with the following main objective: to assess whether WD is a good predictor of the competitive ability of individuals in tree populations. To accomplish this objective, I quantified, at the individual level, sapwood ( $WD_{sap}$ ) and heartwood densities ( $WD_{heart}$ ), sapwood proportion ( $Sap_p$ ), growth rates ( $BAI_{10}$ ) and growth efficiency (GE). Given that sapwood and heartwood differ in functionality, I used  $WD_{st}$ , a standardized way of computing WD that considers both wood type proportions in the stem. In order to determine the relationship between growth rate ( $BAI_{10}$ , a proxy of competitive ability) and WD at the intraspecific level, I analyzed the effect of contrasting access to resources (dominant versus suppressed individuals) and WD fitting mixed-effects correlation models (LMM).  $WD_{st}$  showed very low variation (<6% of CV), and  $WD_{st}$  did not differ between dominant and suppressed individuals for both species, nor did  $Sap_p$ . Dominant individuals of both species had significantly higher  $BAI_{10}$  and GE values than suppressed individuals. I found a non-significant correlation between  $BAI_{10}$  and  $WD_{st}$ . Independently of tree species and access to resources,  $WD_{heart}$  was significantly higher than  $WD_{sap}$ . In conclusion, my results are unequivocal in that WD is a poor predictor of competitive ability among individuals of the same species and thus interspecific trends found in the growth–WD relationship are not paralleled at the intraspecific level.

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## 1. Introduction

Competition between immediate neighbors has been regarded as the most important force of natural selection that shapes the species composition, diversity and evolution of plant traits within plant communities (Tilman, 1982; Silvertown and Charlesworth, 2001). In high-density plant populations, and in the absence of manifested stressors (e.g. fire, insect outbreaks, drought), self-thinning is a dynamic process caused by competition to preempt limited resources that ultimately result in a predictable decrease of density with time (i.e. mortality). Nowhere is this more evident than in forests, where competition for light has profound effects on tree performance leading to mortality and declines in density (Coomes and Grubb, 2000; Freckleton and Watkinson, 2001). According to Oliver's model of forest stand dynamics (1981), the stem exclusion stage occurs when all growing space is

occupied and competition is the highest. At this stage, competition leads trees to markedly differentiate in crown or social classes, where some trees have full access to resources (particularly light), and consequently grow disproportionately larger (dominant individuals) taking growing space from others (suppressed individuals) and forcing them to grow more slowly and ultimately to die (asymmetric competition *sensu* Weiner, 1990). In these tree populations, the effect of conspecific neighbor density on growth is strongest because they should represent the highest niche overlap (Fajardo and McIntire, 2011).

Wood density (WD) is a relevant plant functional trait that is under strong selective pressure as it is important to the survival and growth of a species in its environment (Falster, 2006; King et al., 2006; Preston et al., 2006). WD reflects the balance between solid material (i.e. cell wall, parenchyma) and void (i.e. lumen of conductive elements) of the xylem tissue. As such, WD is a carbon-investment trait resulting from a trade-off involving construction costs (Swenson and Enquist, 2007). The trade-off is

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defined by the impossibility of filling the same volume with cell wall material and cell lumen (Carlquist, 1975; Méndez-Alonzo et al., 2012). In the wood economics spectrum (WES, Chave et al., 2009), species having wide conduits and low WD also have high growth rates (resource-acquisitive extreme of the spectrum), whereas species having narrow conduits and high WD also have low growth rates (resource-conservative extreme of the spectrum) (e.g. King et al., 2005, 2006; Chave et al., 2006, 2009). In this line, there is sufficient support to state that WD scales negatively with leaf gas exchange and water balance, and therefore growth (e.g. Santiago et al., 2004; Pratt et al., 2007; Scholz et al., 2007; Meinzer et al., 2008); WD may mediate a growth–mortality trade-off in tree species (Wright et al., 2010). In a global-comparison study, Chave et al. (2009) found strong negative correlations between WD and both growth rates and mortality: species with higher WD grow slower and live longer. In contrast to the previous general trends, Kunstler et al. (2012) tested the competitive-trait hierarchy hypothesis—initially based on the competitive-ability hierarchy hypothesis (Mayfield and Levine, 2010)—and found that neighboring species with higher WD values than target species had greater competitive effects than species with lower WD. This implies that competitive species (presumably species with high growth rates) were the ones having high WD. However, whether these global patterns are mirrored within species have been poorly explored. All of the mechanistic hypotheses proposed to explain global patterns of WD variation across species should in principle apply within species as well (Fajardo, in press). And yet, empirical evidence suggests that WD is a very conservative trait across large-scale environmental gradients, i.e. it shows very low variation at the intraspecific level (Chave et al., 2009; Fajardo and Piper, 2011; Zhang et al., 2011).

If there is any leeway for WD to vary at the intraspecific level, this should occur within the stand where trees with different access to resources (i.e. different social status) exhibit markedly different growth rates and sapwood-to-heartwood proportions. Sapwood in stems corresponds to the younger, outermost water-conductive area in the trunk, and it is in direct connection with both the leaves and younger roots (Bresinsky et al., 2013). The more foliage a tree can bear and the more vigorous its growth, the larger the sapwood area is required (the Huber value, Tyree and Ewers, 1991; Olson et al., 2009). Dominant trees in a forest stand with a better access to light should exhibit a higher sapwood-to-heartwood proportion than co-dominant and suppressed trees, which have less access to resources. Given that in some tropical forests WD was found to increase with distance from the pith (e.g. Wiemann and Williamson, 1989a, 1989b; Parolin, 2002; but see Hietz et al., 2013), i.e. sapwood density is lower than heartwood density, then dominant trees should show on average lower WD than less dominant tree social classes. The magnitude of these potential differences in WD at the stand level has not been quantified yet.

With most studies of wood traits focusing on the comparative level—where the assumption of the trait-based approach for plant ecology is that trait variation between species should be higher than within species (McGill et al., 2006)—the exploration of intraspecific trait variation (ITV) at the population level due to plant–plant interaction processes has remained largely unexamined. The aim of this study was to quantify the intraspecific variation in WD of tree populations that are under strong competition, and to determine if the predicted negative relationship between growth rate and WD found at interspecific levels also exists at the intraspecific level. In particular, I pursued to assess whether WD is a good predictor of the competitive ability of individuals in tree populations. To accomplish these objectives, I also examined other complementary wood-related traits like sapwood-to-heartwood proportion, growth rates and growth

efficiency. I determined sapwood and heartwood densities as both tissues have different functions in the stem, and apparently differ in densities (Wiemann and Williamson, 1989a,b; Parolin, 2002; Nock et al., 2009; Hietz et al., 2013). Here I developed a simple methodology to obtain a standardized measure of WD per individual that considers sapwood and heartwood proportions in the stem cross-sectional area. In this respect, most studies, albeit assuming that sapwood and heartwood may not differ in their densities, have just considered an unspecified WD value for an individual or species. In particular, if heartwood density is higher than sapwood density (Wiemann and Williamson, 1989a,b; Parolin, 2002), then I would expect that dominant individuals should have lower WD than suppressed individuals because dominant individuals have a higher sapwood-to-heartwood ratio than suppressed individuals. On the contrary, if heartwood density is lower than sapwood density because higher structural support is needed as trees age (Nock et al., 2009; Hietz et al., 2013), the expectation is that dominant trees will have higher WD than suppressed individuals, supporting the finding of Kunstler et al. (2012).

## 2. Methods

### 2.1. Site and species description

The study was conducted in the Coyhaique Reserve (45°33'S, 71°59'W, 700 m a.s.l.), in the Coyhaique Province of the Aysén Region, Chile. The annual precipitation in this area is on average 890 mm (Coyhaique Reserve weather station, Dirección General de Aguas, 2004–2013, 400 m a.s.l.); the warmest month's mean temperature is 14.2 °C, with a potential evapotranspiration of 584 mm (Luebert and Plissock, 2006). In this particular reserve area, a large-scale human-induced fire in 1950 burned some 600 ha of old-growth *Nothofagus pumilio* – *Nothofagus betuloides* forest. Remnant patches of old-growth *N. pumilio*, and to a lesser extent *N. betuloides*, forests served as a seed source for regeneration on the burnt landscape, which occurred primarily around the margins of burned areas. Within decades, natural regeneration of *N. pumilio* and *N. betuloides* resulted in dense second-growth forests (Fig. 1) around the margins of the burned areas (Fajardo and McIntire, 2010; Fajardo and Gundale, 2015). This sequence of fire followed by formation of second-growth *Nothofagus* forests is pervasive in the region. *Nothofagus betuloides* (Mirb.) Oerst and *Nothofagus pumilio* (Poepp. & Endl.) Krasser (Nothofagaceae) are two broadleaf, light-demanding and seed-masting tree species that extend through a wide latitudinal and altitudinal range in the southern



**Fig. 1.** Depiction of an even-aged, post-fire *Nothofagus pumilio* forest in the Coyhaique Reserve (45°33'S, 71°59'W, 700 m a.s.l.), Chile. The trees of this forest are on average 55 years old, with mean diameter at breast height (DBH, 1.35) for dominant trees of 24.5 cm and for suppressed trees of 12 cm. Although the stem density is high (3000 trees ha<sup>-1</sup>), tree mortality is occurring pervasively (see some dead trees with thin stems without bark).

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