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PERSPECTIVE

Rethinking the value of high wood density

Markku Larjavaara* and Helene C. Muller-Landau

CTFS Global Forest Carbon Research Initiative, Smithsonian Tropical Research Institute, Panama

Summary

1. Current thinking holds that wood density mediates a tradeoff between strength and economy of construction, with higher wood density providing higher strength but at higher cost.
2. Yet the further away wood fibres are from the central axis of the trunk, the more they increase the strength of the trunk; thus, a fat trunk of low-density wood can achieve greater strength at lower construction cost than a thin trunk of high-density wood.
3. What then are the countervailing advantages of high wood density?
4. We hypothesize that high wood density is associated with lower maintenance costs due to lower trunk surface area, as surface area correlates with maintenance respiration.
5. This advantage would be particularly important to long-lived trees and could in part explain why they tend to have high wood density.
6. High wood density has also been associated with lower risk of trunk breakage, xylem implosion and pathogen invasion, but we argue that these relationships are not causal and instead reflect correlated selection on other traits of value to long-lived trees.
7. This revaluation of the costs and benefits of high wood density has important implications for understanding tree life-history evolution, functional diversity, forest carbon stocks and the impacts of global change.

Key-words: bark, construction cost, decay resistance, maintenance cost, trunk respiration, strength, xylem implosion

Current thinking – strength vs. construction cost at a given diameter

Wood density is a key functional trait of woody plant species, and one with important effects on ecosystem processes including carbon storage in biomass and necromass (Chave *et al.* 2009). In general, long-lived climax species tend to have high wood density, while pioneers have low wood density (Muller-Landau 2004). As wood construction cost and strength (resistance to trunk breakage) are both proportional to wood density, the prevailing wisdom holds that high wood density provides the benefit of greater strength but entails higher construction costs and specifically slower growth. According to this line of reasoning, pioneers have light wood because their accelerated life history means that a slowdown in growth is relatively more costly and resistance against rare catastrophic events relatively less valuable. Data reported in dozens of empirical journal articles have been interpreted as support for this thinking (van Gelder, Poorter & Sterck 2006) and the idea is sufficiently well established to be presented as fact in textbooks (Lüttge 2007) and stated as a key example of a tradeoff in the popular literature (Royte 2001). However, there are fundamental problems with this argument, as we show in this article.

Engineering physics – how diameter and wood density affect stem breakage

To understand the inherent influence of wood density on risk of stem breakage for vertically oriented main stems, or trunks, it is useful to compare trunks varying in wood density but identical in mass per unit length, and thus identical in construction cost (Schniewind 1962). This means comparing fatter trunks of low wood density with thinner trunks of high wood density. Trunks of equal mass per unit length have equal resistance to rupture stress – that is, to breaking when stretched from both ends like a rope, because rupture stress is proportional to the product of wood density (fig. 3b in Chave *et al.* 2009) and basal area. However, they differ in their strength as trunks of erect trees, due to the varying distances of the fibres from the neutral axes (for simplicity we ignore shear and growth stresses and assume wood to be homogenous).

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*Correspondence author. E-mail: larjavaaram@si.edu

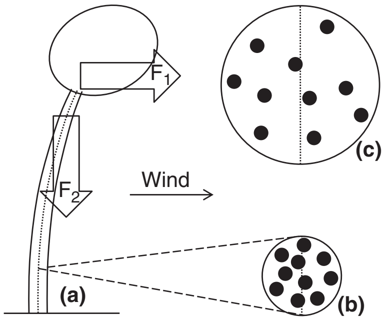

Fig. 1. (a) Wind (F_1) and gravity (F_2) exert forces on a tree and causes its trunk to bend. Cross-sections of two trunks with identical construction cost but fourfold difference in wood density are shown in the same scale in (b) and (c); closed circles represent structural fibres and the thinnest lines represent neutral axes.

Consider two trunks with identical mass per unit length in which one trunk has four times the wood density and half the diameter of the other (Fig. 1b,c). The average distance of fibres to the neutral axis in the larger diameter, lower wood density trunk (Fig. 1c) is twice that in the smaller diameter, higher wood density trunk (Fig. 1b), and thus their average and total resistance to bending is fourfold greater. This is because not only does their moment of resistance to a given bending double (as distance to neutral axis in which fibres are neither stretched or compressed doubles) but also the stretching or compression doubles, doubling the resistance from each individual fibre (in the elastic range). The maximal bending (i.e. maximal stretching in upwind and/or compression in downwind side extreme fibres) of the larger diameter, lower density trunk is half that of the smaller diameter, higher density trunk, and therefore its strength is doubled.

In summary, when comparing individuals of constant construction cost (mass per unit length) but different wood density and diameter, strength is proportional to diameter and resistance to bending proportional to the square of diameter – which means strength is inversely proportional with the square root of wood density and resistance to bending is inversely proportional to wood density (Fig. 2). When comparing individuals of the same wood density, construction cost is proportional to the square of diameter and strength to the cube of diameter.

Paradox in current thinking

Strength and construction cost do increase linearly with wood density, and thus it is true that when comparing trees of identical trunk diameter, those with higher wood density have both higher construction cost and higher strength. However, the conclusion that wood density mediates a tradeoff between strength and construction cost is incorrect, because constant diameter is a misleading basis of comparison. Diameter is easily measured and a convenient basis for categorization. However, it is more useful to compare the benefits achieved for identical costs, or the costs for achieving identical benefits. Such comparisons provide a very different view of the relationship of strength to wood density (Fig. 2). Because strength is proportional to wood density times the cube of diameter, while construction is proportional to wood density times the square of diameter, trees with lower wood density are stronger and more resistant to trunk breakage than trees of higher wood density having the same construction cost. Similarly, trees with lower wood density can achieve the same strength at lower cost than can trees of higher wood density (Anten & Schieving 2010).

Other benefits of high wood density suggested in the literature – flexibility, low implosion risk and resistance to decay

The above arguments show that low-density wood provides higher strength for the same cost and lower cost for the same strength. So what, then, is the countervailing disadvantage? Why do any tree species have high wood density?

A thicker trunk of low wood density is less flexible than a thinner trunk of high wood density having the same strength

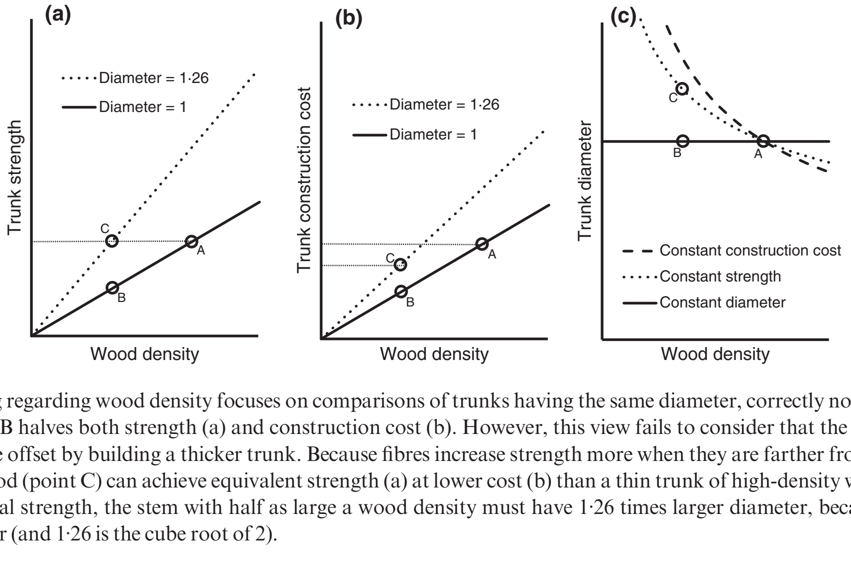

Fig. 2. Current thinking regarding wood density focuses on comparisons of trunks having the same diameter, correctly noting that halving wood density from point A to B halves both strength (a) and construction cost (b). However, this view fails to consider that the decrease in strength of low-density wood can be offset by building a thicker trunk. Because fibres increase strength more when they are farther from the centre, a thicker trunk of low-density wood (point C) can achieve equivalent strength (a) at lower cost (b) than a thin trunk of high-density wood (point A), as seen in (c). Note that for equal strength, the stem with half as large a wood density must have 1·26 times larger diameter, because strength increases with the cube of diameter (and 1·26 is the cube root of 2).

(as explained above). Flexibility (and thus high wood density) is advantageous in reducing the sail area (Vogel 1989), in short gusts of wind intolerable for long periods, in bouncing back after being struck by falling trees or branches and in avoiding liana invasion from neighbouring tree crowns (Forsyth & Miyata 1987). On the other hand, increased flexibility means increased bending for the same force, and the more a trunk bends the further its centre of gravity generally shifts, thus increasing the gravitational forces on the tree stem (F_2 in Fig. 1a). Many attempts to explain tree allometry are based on avoidance of elastic buckling – the collapse of a tree trunk under its own weight due to such vertical forces (McMahon 1973), and this focus makes the paradox in the current thinking even more pronounced (Anten & Schieving 2010). That is, fat stems of low-density wood are much better able to resist buckling than thin stems of high-density wood, even after accounting for the fact that low-density wood has higher water content per dry mass (King *et al.* 2006). But in general, vertical forces are small compared with horizontal forces when the trunk of a mature tree breaks (Niklas 1994; King *et al.* 2009). Thus, it is unclear whether flexibility is advantageous or disadvantageous overall for tree trunks (vertically oriented main stems), our focus here. We consider it unlikely that flexibility is sufficiently advantageous as to be a significant benefit of high wood density.

Wood density affects not only structural support but also the two other aspects of trunk function – storage and transport (Pratt *et al.* 2007). Support requirements are arguably of greatest influence on trunk size and structure: most of the wood of mature trees is dead heart wood which is of no use for transport or storage (Bowyer, Shmulsky & Haygreen 2007), woody climbers have much smaller basal area for a given leaf area (Gerwing & Farias 2000) and wood is constructed of vertical fibres composed in large part of cellulose (for its density 'the strongest material known') providing extreme strength parallel to the trunk (Niklas 1992). Despite this, if storage and transport services correlate strongly with wood density, they could reveal the 'missing benefit' of high wood density. However, we consider it unlikely that storage is widely important in the evolution of wood density. Moreover, because low-density wood has higher storage capacity than high-density wood, storage would, where significant, be another factor favouring low wood density.

It has been postulated that high wood density may aid in the transport of liquids in dry conditions. Hacke *et al.* (2001) showed that wood density correlates positively with the ability of thick conduits to resist implosion, and concluded that high wood density is advantageous for survival in dry climates. However, wood density does not correlate with implosion resistance in roots (Pratt *et al.* 2007), as it should according to this hypothesis. Further, most of the trunk of a typical angiosperm is composed of non-conducting fibres – only a tiny portion of the trunk tissue mass participates in or ever participated in transportation of liquids. It would thus seem that selection could act to strengthen conduit walls to better resist implosion without affecting most of the tissue (the non-conducting parts). As a result, we consider it unlikely that hydraulic safety could have major influences on overall wood density, except possibly for conifers, which do not have specialized conducting vessels (Bowyer, Shmulsky & Haygreen 2007).

Trunks not only need to provide structural support, transportation and storage at a given moment but they also need to survive to provide these services in future. Common sense holds that high-density wood decays more slowly than low-density wood (for a piece of given dry mass), suggesting another possible advantage of high wood density. Wood science confirms that wood density and decay resistance are positively correlated among angiosperm species (Chave *et al.* 2009). It is likely this measure of resistance to decay in dead wood also correlates with defence against pathogen invasion in living trees, and thus with a tree's ability to maintain the integrity and strength of its wood and ultimately its fitness. Assuming this is the case, does higher density itself make wood more resistant to attack? We certainly expect decay resistance to correlate with the concentration of defensive 'secondary compounds' and variation in the concentration of these compounds contributes to variation in wood density. However, given that such compounds normally represent less than 5% of dry mass (Bowyer, Shmulsky & Haygreen 2007), their contribution to wood density variation is very small. This leaves us with the question of whether there is any remaining influence of wood density to resistance of living trunks to attack by animals and microbes, after factoring out the contribution of secondary compounds and possibly variable cellulose to lignin ratio. It is difficult to think of plausible mechanisms for such a relationship given what is known about fungal ecology (Dix & Webster 1995). One potential mechanism is that high-density wood confers a lower risk of wounding and subsequent pathogen attack (Romero & Bolker 2008) when debris fall from above (King 1987), an advantage that would be more significant for long-lived and understorey trees (van Gelder, Poorter & Sterck 2006). Another possibility is that in high-density wood a given proportion of wood mass of secondary compounds goes further because more of the fibre surface area is covered by other fibres. A third possibility is that high-density wood decays more slowly because there is less surface area on which spores can land and more solid structures can penetrate between the bark and centre. However, we consider it unlikely that any of these mechanisms would have substantial influence on wood density evolution.

New hypothesis – the importance of trunk surface area

We argue that none of the four mechanisms discussed above reveal a substantial 'missing benefit' of high wood density. We propose that the most important benefits relate to the reduced trunk surface area of trunks of high wood density. Trunks of high-density wood are thinner than equal strength trunks of low-density wood, and thus have lower surface area. This reduced surface area reduces costs of both bark construction and trunk maintenance.

Bark consists of living inner bark and dead outer bark. Because trunks of high-density wood require less bark, they have lower associated construction costs (David A. King, pers. comm.). These costs are particularly important for small trunks (because bark constitutes a greater proportion of total trunk mass at small diameters) and in ecosystems in which trees need thick bark for protection from fires or herbivores. This mechanism reveals a clear benefit of high wood density and would predict that fire-adapted trees with expensive insulating bark would have higher wood density than others. However, in the case of large trees, it seems unlikely that bark construction costs would ever be sufficiently large to make total trunk construction costs for a given strength lower for a high-density trunk than for a low-density trunk.

Physiological studies have found that trunk maintenance respiration is better predicted by trunk surface area than by sapwood volume (Bosc, De Grandcourt & Loustau 2003). We propose that the most important ‘missing benefit’ of high wood density is in large part the reduction in trunk maintenance costs (energy spent per unit time), which we suggest is proportional to trunk surface area. Specifically, we hypothesize that fat trunks of low-density wood have higher maintenance costs than thinner trunks of high-density wood having the same construction cost, or those having the same strength.

Under this new hypothesis, as in the traditional view, wood of low density represents a prioritization of short-term gains over long-term benefits – but for a completely different reason. The advantage of low-density wood is achieving needed strength at low construction cost; the disadvantage is higher maintenance obligations. Because pioneers have a short life cycle, the maintenance cost is relatively less important, and the benefit of fast growth enabled by the low construction cost for a given strength of low wood density relatively more advantageous. Long-lived climax species, on the other hand, are better off investing in high-density wood that has lower maintenance cost even though it is more expensive and thus slower to build for a given strength.

Conclusions and directions for future research

We have shown that the current explanation for why pioneers have low wood density is faulty. Low wood density does not reflect a prioritization of construction economy over strength – it actually offers higher strength at lower cost than does high wood density (an argument independently developed by Anten & Schieving 2010). We suggest that variation in wood density can best be explained by focusing on strength, construction cost and the maintenance costs of trunk surface area – with lower wood density leading to higher maintenance costs but lower construction cost for the same strength.

In addition, we argue that low wood density does not in and of itself cause trees to be inherently more vulnerable to trunk breakage in high winds (Curran *et al.* 2008), pathogen attack (Romero & Bolker 2008) or drought-induced mortality (Hacke *et al.* 2001). Pioneers prioritize short-term gains over long-term costs and risks in general – and thus tend to not only have low wood density but also low trunk safety margins against breakage in a gale, low investment in protective secondary compounds and poor survival in droughts. We suggest that the observed correlation of wood density with resistance to implosion, decay and breakage is largely a reflection of correlated evolution on different sets of traits whose utility varies in parallel with life history. That is, the long-lived species that benefit from investing in high wood density also benefit from investing in implosion-resistant hydraulic systems, efficient chemical defences and high ratio of trunk strength to leaf area of a tree. The high risks taken by pioneers amplify the difference in growth potential that result directly from differences in wood density, and also increase mortality.

Both the current thinking and our new hypothesis predict that pioneers will have lower wood density, consistent with empirical data (van Gelder, Poorter & Sterck 2006). Our demonstration of the problems with the current thinking follows simply from fundamental physical relationships, as also shown by Anten & Schieving (2010), and does not require further empirical testing. In contrast, our new hypothesis is uncertain, mainly because the substantial respiration of trunk surface indicated by some studies remains poorly understood. Future work in plant physiology and biochemistry is needed to better quantify variation in trunk maintenance costs and elucidate the underlying mechanisms. Such research could include individual tree measurements of carbon efflux along a tapering trunk below the lowest living branch, and stand-level measurements of respiratory fluxes in plantations of species or genotypes differing in wood density.

Appropriate consideration of the costs related to constructing and maintaining trunk surface can provide insight into other ecological questions as well. For example, the expense of trunk surface area could in part explain why stilt and aerial roots and buttresses are rare, or in fire-adapted ecosystems typically non-existent, despite large benefits in strength with small investment in additional wood. Similarly, the decrease in respiration per unit biomass with increasing size among large trees (Mori *et al.* 2010) and the form of the self-thinning law (the way in which total biomass per unit area decreases with increasing number of individuals per unit area) can be explained by accounting for trunk surface respiration (M. Larjavaara, unpublished). Wood of roots, lianas and shrubs provide similar storage and transportation services for the plant as tree trunks but differ radically in their role for mechanical support. Theoretical, physiological and anatomical comparisons between these wood types would help us to better understand the evolution of wood traits.

It has been hypothesized that anthropogenic global change may be resulting in a shift towards species having lower wood density (Laurance *et al.* 2004). Any shift in average wood density could lead to major changes in forest carbon pools (Bunker *et al.* 2005), but previous work has not considered likely coordinated changes in trunk volume. A better understanding of the tradeoffs trees face, one that correctly encompasses strategies varying in both trunk volume and wood density, is needed to interpret variation in wood density, tree size and biomass among species and forests today, and better predict how forests will change in future.

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