

REVIEW AND
SYNTHESIS

Towards a worldwide wood economics spectrum

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Abstract

Wood performs several essential functions in plants, including mechanically supporting aboveground tissue, storing water and other resources, and transporting sap. Woody tissues are likely to face physiological, structural and defensive trade-offs. How a plant optimizes among these competing functions can have major ecological implications, which have been under-appreciated by ecologists compared to the focus they have given to leaf function. To draw together our current understanding of wood function, we identify and collate data on the major wood functional traits, including the largest wood density database to date (8412 taxa), mechanical strength measures and anatomical features, as well as clade-specific features such as secondary chemistry. We then show how wood traits are related to one another, highlighting functional trade-offs, and to ecological and demographic plant features (growth form, growth rate, latitude, ecological setting). We suggest that, similar to the manifold that tree species leaf traits cluster around the ‘leaf economics spectrum’, a similar ‘wood economics spectrum’ may be defined. We then discuss the biogeography, evolution and biogeochemistry of the spectrum, and conclude by pointing out the major gaps in our current knowledge of wood functional traits.

Keywords

Evolution, functional ecology, plant economics, trade-offs, wood.

Ecology Letters (2009) 12: 351–366

1. INTRODUCTION

The arborescent life-form arose out of an evolutionary arms race for the capture of light. By positioning leaves above those of its neighbours, a tree is able to intercept a large proportion of solar radiation and puts itself at strong selective advantage (Falster & Westoby 2005). Jostling for a larger share of resources by locating leaves upwards on woody stems provided impetus for the evolution of trees that today dominate several terrestrial biomes. The woody tissues of trees and other plants perform three important functions. They provide biomechanical support for the stems that suspend photosynthetic tissues above the ground (Rowe & Speck 2005),

they conduct water and nutrients along the soil–plant–atmosphere continuum (Tyree & Zimmermann 2002; Sperry *et al.* 2008), and they act as a store for nutrients, carbohydrates, defensive secondary chemical compounds, lipids and water (Harmon *et al.* 1986; Kozłowski 1992). Because wood performs more than one task, there are conflicting demands on wood structure and these demands may shift depending upon the environment. Over the course of evolution, novel cell types have arisen, and variation in the size, form, arrangement and frequency of these cell types has given rise to a diversity of woods that perform these functions across a range of ecological settings (Feild *et al.* 2000; Carlquist 2001; Choat *et al.* 2008; Sperry *et al.* 2008).

Impressive advances have been made in understanding plant ecological strategies by focusing on leaf traits, but less attention has been paid to wood traits. Wright *et al.* (2004) drew from a global database of leaf functional traits to show that these traits co-vary in a way that depends little on environmental features: short-lived leaves have low leaf mass per unit area, high nutrient concentrations and high photosynthetic rates per unit mass while the converse is true of long-lived leaves. They called the manifold of traits around which all species cluster the 'leaf economics spectrum', which depicts the major trade-offs plants are facing when they produce leaf tissue, be they defensive, physiological or structural. Other conceptual frameworks of plant ecological strategies have placed emphasis on both photosynthetic and reproductive traits. Westoby *et al.* (2002) argued that the leading dimensions of ecological variation among plants include leaf traits (leaf mass per area, leaf lifespan, leaf size), stem traits (leaf size–twig size ratios), seed traits (seed mass, seed output) and whole-plant morphological traits (total plant height). Wood traits were not explicitly considered in these earlier studies, but they have been discussed more recently (Westoby & Wright 2006).

An increased understanding of xylem function is highly relevant to biogeochemistry and ecosystem ecology, as plants make up over 90% of the living biomass stock, and the carbon stored in the highly lignified cells of both living and dead stems is a crucial component in the global carbon cycle (Denman *et al.* 2007). Knowledge of the factors limiting the decomposition of wood is critical to understanding whether forests are net sinks or sources of carbon. Indeed, the reduction in woody plant cover over large geographical areas as the result of land-use changes, fire, insect or pathogen outbreaks, releases globally significant quantities of greenhouse gases into the atmosphere (Denman *et al.* 2007; Kurz *et al.* 2008). One challenge has been to scale up from the dynamics of groups of interacting individual trees to regional carbon budgets in terrestrial ecosystems (Purves & Pacala 2008). Complicating this challenge are recent findings that suggest it is essential to have some basic information of wood properties, in particular wood density, to obtain reliable estimates of carbon stocks in the major terrestrial biomes (e.g. Baker *et al.* 2004). Therefore, the importance of variability in wood functional traits requires more scrutiny.

In this review, we seek to identify the leading dimensions of ecological variation among plant traits related to wood structure and organization (Baas *et al.* 2004; Wright *et al.* 2006a; Zanne *et al.* 2006; Wheeler *et al.* 2007) by reviewing research on wood anatomy, biomechanics, ecophysiology and biogeochemistry. We have collated a number of existing databases from the plant taxonomy and wood technology literature to explore the major axes of variation in wood

traits. We use these data to explore whether there is a 'wood economics spectrum' – a manifold of co-varying wood traits around which species cluster. Four steps are needed to define such a wood economics spectrum. First, we must identify a set of wood traits that have important influences on ecological processes. Second, we must check whether these traits co-vary, and thus point to potential trade-offs. Third, we must determine whether these co-variations are reflected in allocation decisions (real trade-offs), providing a firm basis for interpreting such a spectrum within an economics context (costs and benefits). Fourth, studies of plant functional traits often focus on trade-offs and correlations of traits within a given plant organ, but plants maximize fitness by making allocation 'decisions' that optimize growth and survival across all tissues. Thus, it seems likely that wood traits should ultimately be integrated with other trait spectra and these combined allocations should lead to predictable differences in growth and survival.

In the forthcoming sections, we explore the functional properties of wood (Section 2); we then examine correlations among wood traits and look for evidence of coordination and trade-offs between wood traits and other plant traits (Section 3). Armed with this knowledge we look at the extent to which wood traits are related to emergent demographic properties of plants: growth and mortality (Section 4). Finally, we explore the biogeographical, evolutionary (Section 5) and biogeochemical (Section 6) implications of our findings.

2. LEADING DIMENSIONS IN WOOD FUNCTION

A. Wood density as an integrator of wood properties

Wood density, defined here, is the oven-dry mass divided by green volume. It has traditionally been regarded as a key functional trait by ecologists. The density of woody structures excluding open spaces in wood is *c.* 1.5 (Siau 1984), hence wood density is bounded by 0 and 1.5 g cm⁻³. Wood density thus also describes the carbon investment or carbon storage per unit volume of stem (see Section 5).

Wood density varies within individuals. As wood ages, the inward part of sapwood is converted into heartwood (duramen) through the polymerization of compounds such as lignan, stilbene and flavonoid derivatives (Hillis 1987; Schultz *et al.* 1995). Heartwood xylem lacks functional conduits and parenchyma. Foresters typically measure heartwood density, yet sapwood (xylem containing functional conduits and parenchyma) densities are often significantly lower than heartwood densities (Woodcock & Shier 2002; Patiño *et al.* 2008). This pattern has been attributed to the structural support required at different ontogenetic stages or changes in chemical deposition in heartwood.

Furthermore, wood density varies with height within the plant (Swenson & Enquist 2008). The wood density of roots has not been measured as extensively as stems; however, roots tend to have lighter wood (Pratt *et al.* 2007).

Given the perceived importance of wood density with mechanical support, water transport and storage capacity of woody tissues, we have assembled the largest compilation of wood density data to date, encompassing 8412 taxa, 1683 genera, 191 families (for more details on database construction, see Appendix 1 in the Supplementary Online Information). The dataset is available in the Dryad data repository (<http://datadryad.org/>). In the forthcoming sections, we will also discuss geographic, phylogenetic and ecological patterns related to wood density.

B. Water transport in the xylem

One of the major roles of xylem in land plants is to transport sap to the leaves and photosynthate to the plant organs (Kozlowski 1992). This places important constraints on the architecture of stems (Tyree & Zimmermann 2002; Sperry *et al.* 2008). Vessel elements represent the most important water conductive cell types in angiosperms (Glossary, see Supplementary Online Information). Vessels vary in length from a few millimetres up to several metres, and they vary in diameter from < 20 to $> 500 \mu\text{m}$, while cross-sectional area percentages of vessels range from 4% to 60%. The degree to which vessels are connected to each other can influence both rates of water transport and ability to deal with xylem dysfunction, or embolism (Fig. 1, Zanne *et al.* 2006; Choat *et al.* 2008). In general, vessel length is positively correlated with vessel diameter (Ewers *et al.* 1997; Hacke *et al.* 2006). In conifers, which lack vessels, *c.* 95% of the constituent cells are long, fibrous tracheids, a more primitive cell type than vessel elements (Carlquist 2001). Tracheids vary in length from < 1 to > 5 mm, and from < 10 to $> 50 \mu\text{m}$ in diameter. Water transport in conifers mainly occurs via wide earlywood tracheids, and mechanical support mainly occurs via narrow latewood tracheids. The relative distribution of angiosperms and conifers is likely related to differences in their wood properties (Sperry *et al.* 2008). For instance, it has been suggested that in lowland tropical environments, angiosperms have out-competed conifers because of their innovations in hydraulic transport (Bond 1989).

At the conduit level, the efficiency of water transport can be mechanistically described by the Hagen-Poiseuille equation, which relates the theoretical hydraulic conductivity K of a conduit assuming a laminar flow (Appendix 2). The longer and wider the conduit is the lower is its resistance to water flow. At the same time, increased conduit diameter greatly decreases safety, especially with respect to freezing-induced cavitation. This represents what some believe to be

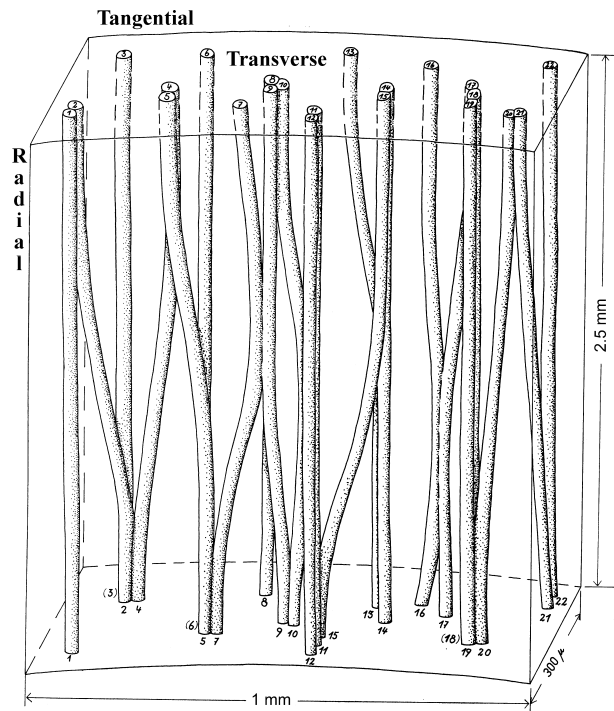


Figure 1 Xylem structure and water transport. This figure shows a reconstruction of the vessel network in *Populus* based on serial sectioning. A particular vessel may jump from one vessel group to a solitary position or to another vessel group. Modern technology enables a rapid analysis of the vessel network by 3D X-ray computed microtomographic reconstruction. Modified from Braun (1970) with permission from Borntraeger-Cramer.

an important trade-off in plant function (Baas *et al.* 2004). At the whole-plant level, simple theoretical models have been constructed to simulate how ideal plants should work. Such models include the classic pipe model (Tyree & Zimmermann 2002), the West–Brown–Enquist theory for water conduction in plants (West *et al.* 1999), and Murray's law (McCulloh *et al.* 2004).

The vulnerability of xylem conduits to cavitation is empirically assessed through a number of methods, which often consist of estimating the xylem tension (negative pressure) at which 50% of the conductivity is lost (Ψ_{50} , see Tyree & Zimmermann 2002). Ψ_{50} varies greatly among species, from -0.18 MPa to -14 MPa, with larger absolute values in conifers than in angiosperms (Maherali *et al.* 2004). Based on empirical evidence, there is general agreement that the primary cause of water stress-induced embolism is penetration of air through pit membranes, a process known as 'air-seeding'. Increasing porosity of pit membranes makes water transport more efficient, but it also makes transporting elements more vulnerable to air-seeding. Recent studies have suggested that it is the total area of intervessel pit membranes in a vessel rather than the individual pit

structure that is most important in determining a vessel's cavitation resistance and transport efficiency (Hacke *et al.* 2006).

How do conduit properties co-vary? The frequency of conduits mm^{-2} was correlated negatively with the mean diameter of those conduits across a wide range of conifer and of angiosperm species (fig. 1a in Sperry *et al.* 2008). This is in agreement with the idea that fewer wide conduits than narrow ones can pack into a unit area of stem. Second, sapwood area hydraulic conductivity K_S (conductivity per unit of cross-sectional sapwood area) also scales with conduit diameter in conifers and angiosperms, and the scaling is consistent with the Hagen-Poiseuille equation (Fig. 2a, see also Sperry *et al.* 2006). This equation places a ceiling on the value of K_S (solid line labelled lumen conductivity in Fig. 2a), as in reality the laminar flow of water in conduits has been measured at anywhere from 20% to 100% of theoretical conductivity. Third, typically water molecules must pass between many thousands of conduits in order to move from the roots to the canopy. Hence, in addition to the resistance imposed by the conduits, water will encounter resistance imposed by conduit end walls. The resistance accounted for by end walls is $\sim 50\%$ of total xylem hydraulic resistance, suggesting that pit structure in end walls plays an important role in the overall hydraulic efficiency of plants (Choat *et al.* 2008). Finally, only a weak relationship has been found between sapwood area hydraulic conductivity K_S and Ψ_{50} (Fig. 2b). In a meta-analysis of the literature, Maherali *et al.* (2004) found that the significant relationship between K_S and Ψ_{50} was primarily driven by the structural difference between conifers and angiosperms. If the two clades are considered separately (or a phylogenetically independent contrast analysis is performed), no correlation was observed. These results suggest that vulnerability to cavitation and hydraulic efficiency are largely independent axes of the wood economy spectrum. Such findings are somewhat surprising as air-seeding is thought to be related to vessel volume and if diameter and length scale then one would expect diameter and vulnerability to be related (Sperry *et al.* 2008).

It is often believed that wood density and water transport efficiency should be correlated because tissue density is related to the amount of space dedicated to conduits. At least in angiosperms, evidence for the relationship between vessel anatomy and wood density is mixed (Preston *et al.* 2006; Pratt *et al.* 2007). The proportions of non-conducting elements, such as fibres, vary greatly among species (Gartner *et al.* 2004). For instance, some angiosperm species with dense wood, such as *Leptospermum scoparium* in New Zealand, contain a scattering of large conduits within a matrix of fibres (Meylan & Butterfield 1978) so may not have especially low conductivity, provided that these conduits remain free from embolism. Additionally, fibres are the

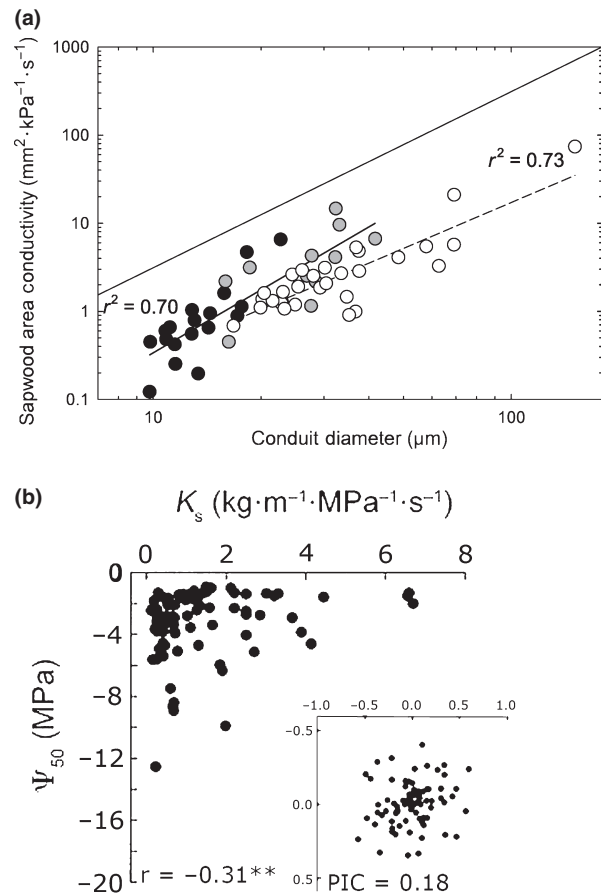


Figure 2 Water transport and wood anatomy. (a) Relation between sapwood area conductivity ($\text{mm}^2 \text{kPa}^{-1} \text{s}^{-1}$) and conduit diameter (μm), from Sperry *et al.* (2006). Closed circles are gymnosperms and open circles are angiosperms. The solid line across the plot represents the theoretical conduit conductivity. (b) Relation between xylem area conductivity ($\text{kg m}^{-1} \text{kPa}^{-1} \text{s}^{-1}$) and vulnerability to cavitation (as xylem tension at which 50% of conductivity is lost, MPa). The relation between these variables was negative and significant (main panel, $n = 168$). Phylogenetic independent contrasts (PIC) of these two traits are plotted in the inset. Unlike the traits, the PICs were not correlated, showing that the two traits showed no concerted evolution. Modified from Maherali *et al.* (2004).

main tissue providing mechanical strength in angiosperms. Fibre wall thickness can vary across species and is typically a strong correlate of wood density (Pratt *et al.* 2007). We computed the mean wood density for the species with very thin-walled fibres and those with very thick-walled fibres, and found that species with very thick-walled fibres had a significantly higher mean wood density than species with very thin-walled fibres (Appendix 3). Furthermore, wood density is typically negatively related to capacitance, the ability of wood to store and release water under tension (Jacobsen *et al.* 2007; Pratt *et al.* 2007; Sperry *et al.* 2008).

Wood density then is related to transport safety if not transport efficiency.

C. Mechanical properties

Plant shape is limited by structural constraints of mechanical stability against bending and buckling (Niklas 1995). The ability of plants to resist bending or breakage should be important across different ecological settings, depending on the likelihood of environmental disturbances. The elasticity to bending is measured by Young's modulus (modulus of elasticity), defined as the ratio of stress over strain, in MPa. If too large a stress is applied to a material, it loses its elasticity, and eventually breaks. The stress needed to reach this point is called modulus of rupture (also in MPa). Other quantities have been routinely reported in the wood mechanics literature, including the dynamic resilience to breakage and the resistance to splitting (Appendix 4). These measures may also be of relevance to ecological studies. Additionally, denser wood is known to convey greater mechanical stability (Niklas 1995; Jacobsen *et al.* 2007; Pratt *et al.* 2007; Poorter 2008). Figure 3 reports the correlation of four wood mechanical traits with wood density among angiosperm species. A significantly positive correlation was found in all four cases.

How do these standard wood measurements relate to the conditions encountered by living trees in the field? Surprisingly few publications address this topic (Niklas 1993; Jacobsen *et al.* 2007; Pratt *et al.* 2007; Poorter 2008). van Gelder *et al.* (2006), however, reported figures for Young's modulus ranging between 2000 and 8000 MPa, and

modulus of rupture between 5 and 30 MPa, both in the low range (Fig. 3) compared with laboratory measurements. This discrepancy may be understood by the fact that field samples were measured in wet condition, and Young's modulus is smaller for wet than for dry samples (Mencuccini *et al.* 1997).

D. Defence properties

Plants must defend themselves against their predators and pathogens but also against natural hazards, such as fire, snow or wind. One mechanism of defence after the development of an infection or wound is compartmentalization of decay via a barrier zone made of non-conducting tissue (Shigo 1984; Pearce 1996). Other defence mechanisms, most efficient against animals and pathogens, consist of synthesizing chemicals (Hawley *et al.* 1924). Over 25 000 secondary compounds are known in plants (Croteau *et al.* 2000), and these compounds are believed to be critical for the evolution of plant defence (Agrawal & Fishbein 2006). For instance, the chemical deposition that occurs during heartwood formation helps prevent attack from predators and pathogens (Hillis 1987; Schultz *et al.* 1995). The presence of secondary compounds in hardwood has long been thought to be related to their durability (Hawley *et al.* 1924). However, to our knowledge, a database cataloguing the presence and amount of secondary compounds in wood, especially relative to wood durability is missing; as a result no large cross-species check of this hypothesis is available.

A simple test of this hypothesis is whether coloured (brown or red) hardwoods, richer in secondary compounds,

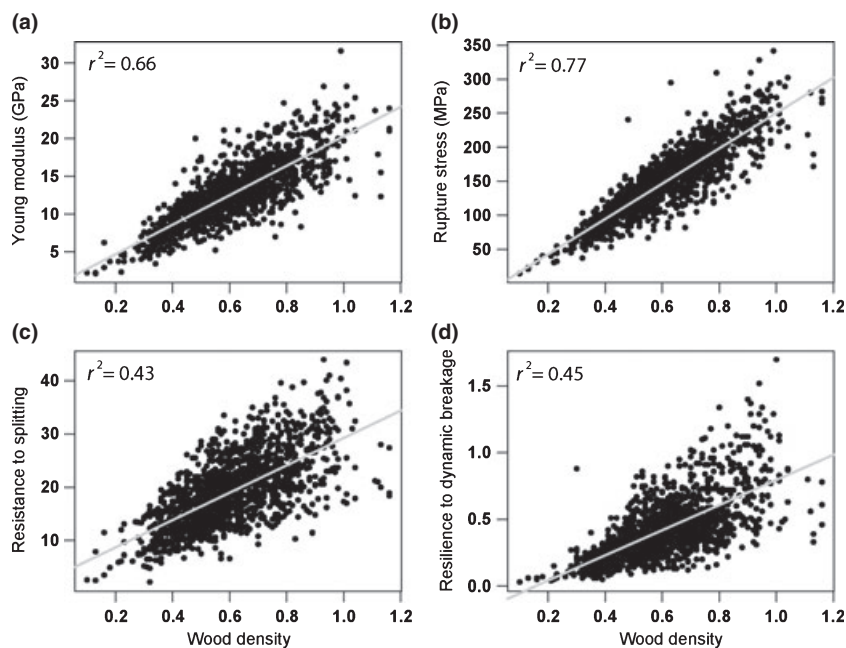


Figure 3 Wood mechanical traits plotted against wood density for 1341 samples from 63 families, 298 genera and 520 species. (a) Young's modulus (GPa, or 10^3 MPa). (b) Modulus of rupture (MPa). (c) Resistance to splitting of a normalized piece of wood along the fibres (kg cm^{-1}). (d) Resilience to dynamic breakage, k , where W is the work needed to completely break a piece of wood. See Appendix 4 for more details. All linear regressions are significant ($P < 0.01$; solid line; r^2 coefficient of correlation is reported in each panel).

are more durable than light-coloured hardwoods. Scheffer & Morrell (1998) reported the durability of wood of many species based on 'graveyard' experiments, where pieces of hardwood were placed in the ground and deterioration status recorded. Heartwood colour is available for some of these species from the InsideWood database. We combined both datasets to show that dark-coloured hardwoods were significantly more resistant to decay than light-coloured ones in agreement with the hypothesis (Appendix 5).

E. The wood economics spectrum

Baas *et al.* (2004) suggested the existence of a 'trade-off triangle' comprised of (i) a negative trade-off between the resistance to embolism (Ψ_{50}) and conductive efficiency, (ii) a negative trade-off between conductive efficiency and mechanical strength and (iii) a positive relation between resistance to embolism and mechanical damage. While the relationships suggested by Baas *et al.* (2004) are intuitive, we suggest that they do not encompass the full range of variation in wood properties (e.g. water and carbon storage and defence properties), so may be missing key components needed for determining the economy of stem structure and function. Furthermore, relationships between hydraulic conductivity and both resistance to embolism and mechanical strength have fairly limited empirical support. Figure 4

summarizes the relations between major ecological functions and the above-mentioned wood traits.

Based upon the evidence presented above, we suggest that a more comprehensive wood economics spectrum may be defined, as the three following points hold. (i) A number of key ecologically-relevant woody stem variables are available (Table 1). (ii) Some of these traits co-vary. With respect to water transport, conduit dimensions correlate with hydraulic conductivity K_h , and wood density correlates with vulnerability to embolism. Several variables describe mechanical properties of wood and these variables relate strongly to wood density. Finally, heartwood colour, a likely indicator of secondary compound deposition, is related to wood durability. (iii) The observed covariation in traits should reflect trade-offs in carbon and nutrient allocation patterns across species.

As discussed above, the existence of a wood economics spectrum depends on a fourth condition, namely that plants

Table 1 The main wood functional traits as measured in the ecological literature, with units and typical ranges

Trait	Symbol	Unit	Range
Wood density	ρ	g cm^{-3}	0.1–1.5
Anatomical			
Number of conduits per cross-sectional area of the xylem	N	No. mm^{-2}	1–1000
Mean conduit diameter	d	μm	10–500
Conduit element length	l	μm	100–5000
Total conduit length	L	cm	0.1–1800
Water flow			
Hydraulic conductivity	K_h	$\text{mm}^2 \text{kPa}^{-1} \text{s}^{-1}$	0.3–200
Resistance to cavitation	Ψ_{50}	MPa	–0.18 to –14
Mechanical resistance			
Modulus of elasticity (MOE)	Y	MPa	500–30 000
Modulus of rupture (MOR)	R	MPa	10–350
Resistance to splitting	S	N m	1–45
Resilience to dynamic breakage	k	NA	0.01–1.8
Chemical			
Proportion of cellulose		%	38–53
Proportion of lignin		%	16–32
Concentration in N		p.p.m.	700–1200
Concentration in P		p.p.m.	50–100
Concentration in K		p.p.m.	500–1000
Concentration in Ca		p.p.m.	700–1200
Concentration in polyphenols (incl. Tannins)		‰	NA
Presence of latex/gums/oils/mucilages		0/1	NA

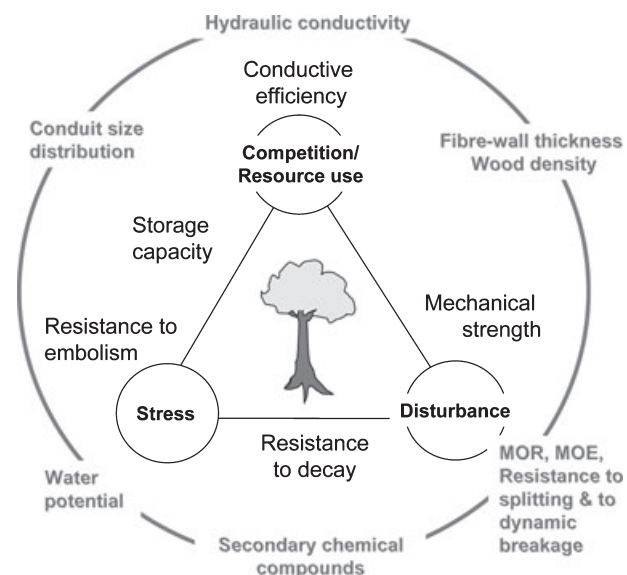


Figure 4 The role of wood in major plant ecological functions (competitive ability, resistance to stress and disturbance). Wood properties are reported around the triangle (see also main text): water transport and storage, mechanical properties and defence properties (resistance to decay and embolism). The outer circle relates the main wood traits associated with these wood properties (see also Table 1).

maximize fitness by making allocation ‘decisions’ that optimize growth and survival across all tissues. The next section presents evidence of coordination and trade-offs between wood traits and other plant traits. We also take the integrator trait of wood density and relate it to the demographic variables of growth and survival to determine how this stem trait may be affecting long-term reproductive success in woody plant species.

3. WOOD TRAITS IN RELATION TO OTHER FUNCTIONAL TRAITS

A. Wood and morphological traits

Potential height has been related to a number of wood traits. Taller plants have bigger conduits in their trunks, but fewer conduits in total (Preston *et al.* 2006), because taller plants have longer path lengths and therefore need wider vessels to maintain hydraulic conductivity (Coomes *et al.* 2008). The presence of wider conduits in tall plants may also be related to biomechanical constraints, which are likely to be more limiting in taller organisms. For instance, wider conduits are more efficient per unit of area leaving more space for supporting fibres. Reported relationships between height and wood density or height and strength are mixed (Falster & Westoby 2005; van Gelder *et al.* 2006; Preston *et al.* 2006; Poorter 2008). Both Niklas (1993) and Poorter (2008) show the importance of density of different anatomical structures and how the distribution of those structures change with height.

Growth form is likely related to wood traits in similar ways to plant height as taller trees would be expected to have larger vessels than shorter shrubs. Wood anatomical features were strongly associated with growth form in a study of chaparral species (Carlquist & Hoekman 1985). Lianas, as parasites of free standing plants, allocate fewer resources to mechanical support (Ewers & Fisher 1991; McCulloh *et al.* 2004). A greater proportion of the cross-sectional area of liana wood may be dedicated to vessels, with the vessels often found to be both wide and numerous (Baas *et al.* 2004). As a result, water transport efficiency of lianas is similar to that of free standing plants (Cernusak *et al.* 2008).

B. Wood and leaf traits

Leaf size decreases with increasing wood density (Wright *et al.* 2007). This relationship could be driven by hydraulics with larger leaves demanding greater sap (Coomes *et al.* 2008). Thus as conduit fraction increases wood density may decrease (although this relationship has been mixed at least for angiosperms; Preston *et al.* 2006; Pratt *et al.* 2007). The pattern between leaf size and wood density may instead be

part of a whole-plant strategy with species with larger leaves having faster volumetric growth and lower wood density. Alternatively, this relationship between wood density and leaf size may be due to both traits being related to the amount of leaf area deployed per unit of stem (Wright *et al.* 2007). Denser wood tends to be found in species with thinner branches (Sterck *et al.* 2006) and lower leaf area per stem mass or per stem area (Ackerly 2004; Wright *et al.* 2006b; but see Bucci *et al.* 2004). Species with bigger vessels also typically have more leaf area per sapwood area (Preston *et al.* 2006).

In the leaf economics spectrum, an axis of variation exists in leaf construction from ‘cheap’ tissue investment and fast returns on that investment, to ‘expensive’ tissue investment and slower returns (Wright *et al.* 2004). One might expect that leaf economics traits related to slow returns on investment would be tied to dense wood (Wright *et al.* 2007); however, evidence for such a correlation has been mixed. Santiago *et al.* (2004) found wood density and photosynthetic capacity (A_{mass}) to be negatively related. While two studies found that specific leaf area (leaf area/leaf mass) and wood density were negatively related (Bucci *et al.* 2004; Ishida *et al.* 2008), another found no correlation (Wright *et al.* 2007). Ishida *et al.* (2008) did find wood density to be positively related to leaf lifespan but not to photosynthetic rates. These mixed findings suggest that relationships between stem and leaf function are complex and merit further investigation.

Minimum leaf water potential (the tension measured in leaves during the driest season of the year) has been put forward as a proxy for maximum rooting depth (Ackerly 2004), when comparing species within a given ecosystem. It is assumed that species with deeper roots will have better access to soil water and thus less minimum leaf water potentials (McElrone *et al.* 2004). Wood density has repeatedly been related negatively to minimum leaf water potential (Ackerly 2004; Bucci *et al.* 2004; Santiago *et al.* 2004), and presumably plant rooting depth.

C. Wood and demography

Ultimately, if wood economics trade-offs exist, then wood traits should be related to long-term viability of the plant species, which may be measured by its growth and survival rates.

Growth

There are two reasons to expect that stem growth rates should decrease as wood density increases. First, a smaller volume of wood is, by definition, produced per unit biomass invested in dense wood (Enquist *et al.* 1999; Roderick 2000). Second, dense wood may have a lower conduit fraction, which could result in a lower rate of transpiration,

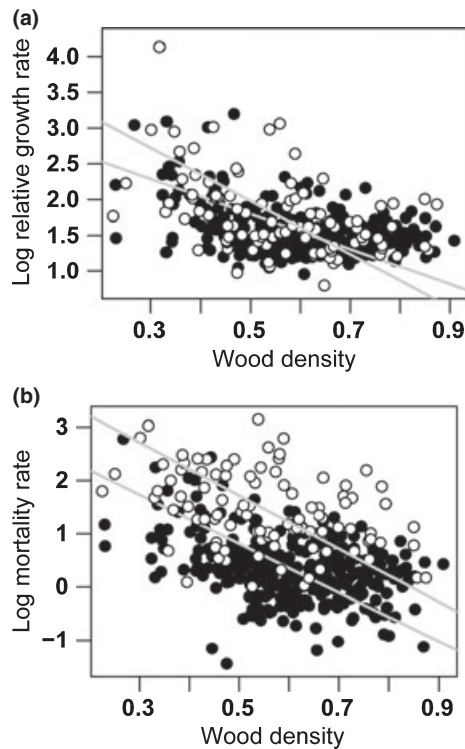


Figure 5 Relationship between wood density and relative growth rate (log-transformed, a), and mortality rate (log-transformed, b), for two tropical forest sites (Barro Colorado Island, Panama, white circles, and Pasoh, Malaysia, black circles). All correlations were highly significant ($P < 0.001$), and the correlation coefficients ranged between $r^2 = 0.13$ and 0.19 . Demographic data were collected from saplings 1–5 cm in diameter under the auspices of the Center for Tropical Forest Science (see Chave *et al.* 2008, and Appendix 6).

photosynthesis and biomass growth (but see Section 2B above). Several studies have reported significant negative correlations between wood density and the mean diameter growth rate of species estimated from permanently marked individuals (Muller-Landau 2004; Nascimento *et al.* 2005; Fig. 5a). However, reported correlations are weak and disappear altogether when a few gap-demanding species were removed from one analysis (Nascimento *et al.* 2005). This result is not surprising given the many factors influencing growth and the different ways in which growth is measured. In comparisons among tree plots, slow growth in diameter was found to be associated with high wood density, e.g. in forests in Amazonia (Chao *et al.* 2008) and Malaysia (King *et al.* 2006). It should be noted that in some instances, having dense wood may lead to greater annual growth rates. Fibres and thick-walled vessels found in high-density wood protect vessels from implosion when water shortage creates strongly negative xylem potentials (Hacke *et al.* 2001a,b). If correct, such an adaptation may allow

heavy-wooded plant species from seasonally dry climates to continue growing when lighter-wooded species are forced into shutting down their water transport systems.

The relationship between growth and wood density has been of great interest to plantation foresters (Fujimoto *et al.* 2006; Bouffier *et al.* 2008; Weber & Sotelo Montes 2008). Breeding trials involve planting genotypes of timber species under similar conditions and comparing their diameter growth and wood density. These trials reveal that intraspecific correlations between growth and density are often weak, or nonexistent, leading to the conclusion that fast-growing genotypes can be selected without compromising on wood quality (Weber & Sotelo Montes 2008). For example, the correlation is inconsistent when all the conifer literature was reviewed (Bouffier *et al.* 2008). A negative correlation between wood density and radial growth rate was found for young hybrid larch, but this relationship weakened considerably with age (Fujimoto *et al.* 2006). Factors other than wood density (e.g. plant age; Fujimoto *et al.* 2006) as well as differences in the way that growth is measured influence growth in these forestry and ecological studies, masking covariance between these two variables.

Survival

High-density wood is associated with low mortality rates in diverse tropical forests (Fig. 5b). Negative correlations between wood density and mortality rate of adult trees have been reported for species in several tropical forests in the Neotropics and Malaysia (e.g. Nascimento *et al.* 2005; King *et al.* 2006; Alvarez-Clare & Kitajima 2007; Osunkoya *et al.* 2007; Chao *et al.* 2008; Fig. 5b; but see Poorter *et al.* 2008). As shown above, wood properties are closely related to mechanical stability, and this function proves critical for survival of trees exposed to disturbance. Curran *et al.* (2008) found that species with low density wood in Queensland were less able to withstand the passing of a severe tropical cyclone. The picture is less clear in temperate regions. Canham *et al.* (2001) reported that early-successional species (purportedly with low density wood) in north-eastern USA were more susceptible to damage than late-successional species, but only when they were small; larger trees were observed to lose many branches in storms but nevertheless survive.

Several patterns emerge from the evidence presented in Section 3. First, free-standing plants with larger vessels are taller and deploy more leaf area per unit sapwood area. Thus plants that are larger both aboveground (and potentially belowground) may have a vascular network with bigger conduits that are able to supply greater total leaf area. Second, wood density correlates with important axes of stem function, and appears to be coordinated with traits across the whole plant, including leaf size, minimum leaf water potential and perhaps rooting depth. Third, wood

density is related to measures of plant performance, especially survival and in some cases growth. A fast–slow continuum of plant performance matches wood traits, with slow growing and lower mortality species having denser wood, smaller leaves, smaller twigs and lower minimum leaf water potentials. It seems likely that these slow growing species should also have higher mechanical strength and/or better chemical defence. Overall, this evidence—albeit indirect—supports important differences in allocation to different stem and whole-plant functions and the existence of a wood economics spectrum.

4. BIOGEOGRAPHY AND EVOLUTION OF WOOD TRAITS

A. Geographical variation of major wood traits

The distribution and diversity of organisms has seldom been explored on large spatial scales upon the basis of their function. A step towards a global scale functional ecology has been to search for consistencies in leaf trait correlations across environments (Wright *et al.* 2004). This step has also been taken for a few of the major wood traits. For instance, along a latitudinal and altitudinal gradient from tropical, subtropical, temperate to arctic or alpine climates, a number of important wood anatomical traits vary. Vessel element length, vessel diameter and frequency of vessel pits (outgrowths from the pit chamber that surround the pit membrane) decrease, while the incidence of scalariform perforations and (fibre-) tracheids increase (Carlquist 2001; Jansen *et al.* 2004; Wheeler *et al.* 2007). Another illustration of wood anatomy shifting with climates is the increasing

frequency of growth rings and ring porosity with seasonality (Wheeler *et al.* 2007).

Wood density has also been shown to vary with latitude: tropical species have similar mean wood densities as temperate assemblages, but with broader ranges and variances (Wiemann & Williamson 2002). This latitudinal pattern also appears to be mirrored along elevation gradients within tropical latitudes with a decrease in the range of values with elevation (Williamson 1984). Our support of these findings is mixed. Table 2 reports the regional cross-species means of wood density, showing that these means vary from *c.* 0.5 g cm⁻³ in temperate regions to over 0.7 g cm⁻³ in subtropical environments.

Variation in wood density has also been examined across climatic and soil nutrient gradients (Wiemann & Williamson 2002; Baker *et al.* 2004; Swenson & Enquist 2007). Analysis of genus-level traits from 277 069 stems across Amazon Basin forests showed a consistent relationship of higher community-average wood density from the North-East of the continent to the South-West, approximately following a gradient in soil fertility and not climate (ter Steege *et al.* 2006). Community-average wood density varied from 0.73 g cm⁻³ in Guyana to just 0.56 g cm⁻³ in Peruvian and Bolivian forests (Malhi *et al.* 2006; ter Steege *et al.* 2006). The regional-scale pattern of species composition and associated wood density therefore define the broad gradient of carbon content of live vegetation across Amazonia (Malhi *et al.* 2006). A negative relationship between wood density and soil fertility appears widespread (Baker *et al.* 2004; ter Steege *et al.* 2006; Patiño *et al.* 2008), as does a positive but weaker relationship between wood density and temperature. There appears to be little relationship between wood density

Table 2 Mean wood density across regions. Wood densities were collected from various sources in the literature (16 468 entries). This dataset has 8412 taxa worldwide (species can occur in more than one of the 16 regions defined below). It is available in the Dryad data repository (<http://datadryad.org/>)

Region	Sample size	Wood density	Standard deviation	Min	Max
Africa (extratropical)	351	0.648	0.159	0.234	1.076
Africa (tropical)	2482	0.598	0.160	0.150	1.200
Australia	678	0.725	0.173	0.300	1.137
Australia/PNG (tropical)	1560	0.636	0.181	0.164	1.227
Central America (tropical)	420	0.560	0.208	0.120	1.350
China	1010	0.541	0.144	0.200	0.996
Europe	77	0.525	0.119	0.284	0.840
India	289	0.652	0.186	0.232	1.280
Madagascar	244	0.662	0.172	0.320	1.164
Mexico	228	0.676	0.231	0.160	1.390
North America	216	0.540	0.153	0.289	1.250
Oceania	110	0.604	0.154	0.270	1.026
South America (extratropical)	744	0.715	0.210	0.120	1.331
South America (tropical)	4191	0.632	0.178	0.100	1.210
South-East Asia	219	0.559	0.154	0.100	0.930
South-East Asia (tropical)	3648	0.574	0.151	0.080	1.095
Total	16 468	0.613	0.176	0.080	1.390

and rainfall (Wiemann & Williamson 2002; Swenson & Enquist 2007).

One recognized weakness is that these observations come from correlations using one-dimensional bi-variate plots in biogeographical analyses of species function. Mapping the distribution of species function in two or more dimensions should be more insightful because climate variables are unlikely to be independently influencing trait values. Here we present an example of this type of approach where we combine geo-referenced herbarium specimen data with the global dataset containing species means for wood density to estimate mean wood density in one-degree grid cells in North and South America (Fig. 6a). We then use this map and underlying climatic data to produce a multiple regression model to predict a smoothed distribution of mean wood densities across these two continents (Fig. 6b). A key finding from this work is that the spatial distribution of this trait cannot be summarized on the basis of a single predictor variable (e.g. latitude). Previous work has predicted the spatial distribution of mean wood densities on a continental scale using a distance decay or inverse weighting method (Swenson & Enquist 2007). The predictive model summarized above explains nearly half of the variation in wood density ($r^2 = 0.49$) suggesting that such an approach could be utilized to generate global scale maps of species function for investigations of biogeochemical cycling and global change modelling (see Section 5). Multiple regression methods such as the one applied here for predictive modelling may be preferred over a distance decay method because there is no *a priori* justification for the decay in trait values with geographical distance.

B. Phylogenetic patterns

Phylogenetic trends in wood anatomy and the systematic significance of various features have been illustrated for a wide range of taxa (Baas *et al.* 2000, 2004; Carlquist 2001). The transformation of vessel element perforation plates from scalariform to simple ones in combination with a decrease in vessel element length is commonly regarded as one of the major trends of secondary xylem evolution established by the Baileyan school (Bailey 1944). This pattern was considered for a long time to be one of the strongest and most reliable phylogenetic trends in plant anatomy. More recent studies on the distribution of vestured pits have illustrated that this character represents another wood anatomical feature with a strong phylogenetic signal in angiosperms (Jansen *et al.* 2004). Although in many cases wood anatomical diversity patterns reflect their phylogenetic significance, there is a considerable amount of homoplasy, which can partly be interpreted as a result of ecological adaptations for water transport and mechanical support (Sperry 2003). Ecological trends in turn can be

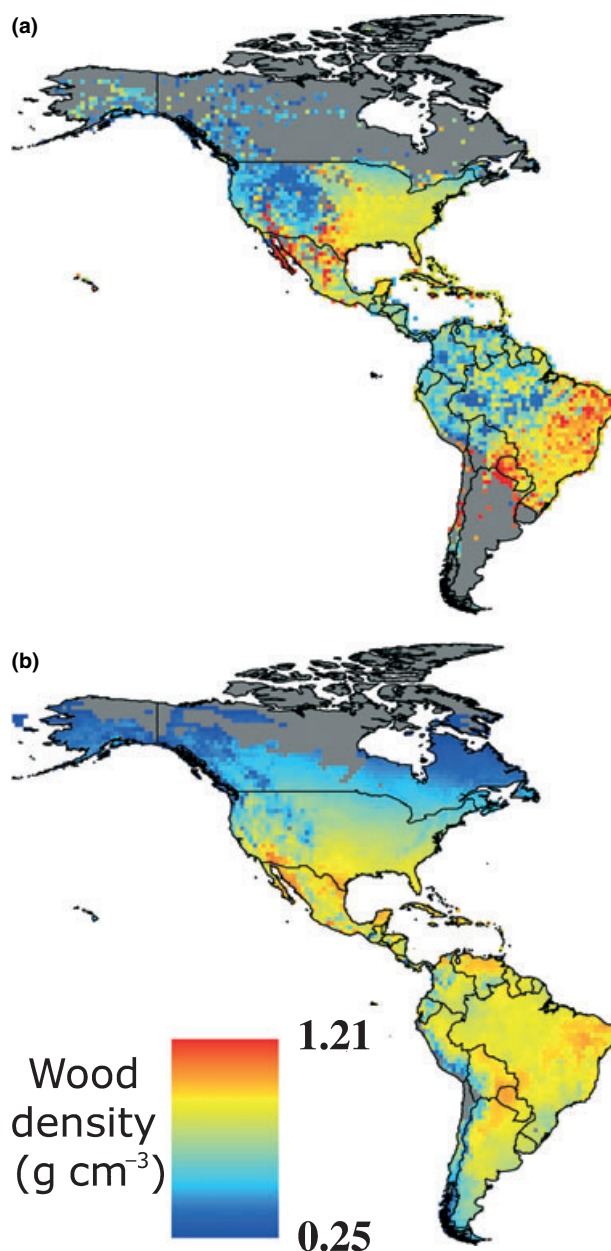


Figure 6 The geographical distribution of wood density in North and South America. (a) Observed mean wood density value in 1-degree grid cells. Grid cell values were calculated by joining the global wood density database to geo-referenced herbarium specimen records from publicly available databases. Each grid cell mean is calculated as the mean wood density value of all unique species occurrences in that cell (i.e. the mean is not weighted by the number of occurrences for each species in that cell). (b) Predicted mean wood density value in 1-degree grid cells on the basis of climatic variables. This predicted map was made using a multiple regression model ($r^2 = 0.49$) where data from panel (a) was the dependent variable, and mean annual temperature, annual precipitation, precipitation seasonality and temperature seasonality were the independent variables (see Appendix 7 for more information on these methods).

understood as functional adaptations when considering trade-offs between structure and function in different growth forms and environments, especially with respect to conductive efficiency, vulnerability to embolism and mechanical strength (Baas *et al.* 2004).

Based on the current consensus of a family-level phylogeny in angiosperms, a strong phylogenetic signal has also been documented in wood density (Chave *et al.* 2006; Swenson & Enquist 2007), meaning that more closely related species share more similar wood density values than less closely related species. Additionally, wood density has shown evolutionary coordination with other plant traits, including seed size (Wright *et al.* 2007) and resistance to drought-induced embolisms and capacitance (Jacobsen *et al.* 2007; Pratt *et al.* 2007).

5. WOOD AND BIOGEOCHEMICAL PROCESSES

A. The carbon cycle

Wood holds ≈ 850 Pg dry mass globally ($1 \text{ Pg} = 1 \times 10^{15} \text{ g}$), equating to a stock of ~ 425 Pg of carbon, a globally significant amount, compared to the current atmospheric stock of ~ 730 Pg C (Denman *et al.* 2007). This carbon stock in wood assumes that the carbon concentration in wood equals 50%. Some uncertainties remain about this figure, however. The carbon content of wood varies with species and possibly location, because species with high lignin content tend also to have higher carbon content (Elias & Potvin 2003; Thomas & Malczewski 2007). Thus, there may also be differences in carbon content depending upon the successional status of the species (Thomas & Malczewski 2007). Volatile organic compounds in wood may add up to 1.6–3.5% of the current estimates of C stocks in wood (Thomas & Malczewski 2007). While these modifiers of the '50% rule' are small, a change of 0.2% would be equivalent to an error of 1 Pg C on the total carbon flux estimate.

The carbon content of individual trees, and hence patches of forest, is critically dependent on knowledge of the tissue density of a given tree. Studies on harvested trees show that wood density is the second most important parameter necessary to accurately predict the mass of a tree, after its diameter, and more important than the height (Chave *et al.* 2005). Recent analyses of Amazonian forests highlight the importance of regional variation in community-averaged wood density in determining carbon stocks (see above). Baker *et al.* (2004) estimated that regional variation in community-averaged wood density accounted for 29.7% or 45.4% of the total variation in aboveground biomass (and therefore carbon content) for plots across Amazonia (depending upon the tree allometry assumed). The 23% decline in community-

average wood density from East to West Amazonia (ter Steege *et al.* 2006) coincides with a threefold increase in wood biomass production (Malhi *et al.* 2004) and forest dynamism (Lewis *et al.* 2004). Such rapid dynamism and low residence time of stems in low community-average wood density forest appear to preclude the accumulation of high carbon stocks.

B. Other biogeochemical cycles

Even though angiosperm wood comprises an average of only 1189 p.p.m. of nitrogen (N) in temperate regions (Harmon *et al.* 1986), and 700–7200 in the tropics (e.g. Kauffman *et al.* 1995; Liu *et al.* 2003), this scales up to > 1 Pg across terrestrial ecosystems. The wood of conifers is less enriched in N (mean: 704 p.p.m.), while bark has up to a fivefold greater concentration in N than wood (Harmon *et al.* 1986). The Ca concentration is comparable to that of N, followed by Mg, K and Mn concentrations, and S and P concentrations (Harmon *et al.* 1986). For P, which may be an important limiting nutrient for many tropical forests, concentrations in wood are lower, at 150 and 250 p.p.m. for four Amazonian and one Asian forest respectively (Kauffman *et al.* 1995; Liu *et al.* 2003). However, surprisingly little data are available on P content of wood, compared to the extensive work on foliar concentrations (Wright *et al.* 2004).

The low concentration of P and N in wood gives exceptionally low Redfield-type molar C : N : P ratios, compared to classic marine Redfield ratios, with wood having lower Redfield ratios than foliage, fine roots, and even leaf litter (McGroddy *et al.* 2004). The low C : N : P ratio of wood suggests that wood may be an important location of the terrestrial carbon sink of $2.6 \text{ Pg C year}^{-1}$ in the 1990s (Denman *et al.* 2007). As plants increase their wood mass, they exert low additional nutrient demand compared to that expected if the same amount of carbon were incorporated into other biological materials. A careful assessment of forest inventory results, taking into account wood density suggest this to be the case, with significant sinks in forest trees (Baker *et al.* 2004; Luyssaert *et al.* 2008; Lewis *et al.* 2009).

C. Tissue turnover

The oxidation of wood is a major flux of carbon from terrestrial to atmospheric pools: tropical forest conversion to other land uses is the second largest anthropogenic source of carbon to the atmosphere after fossil fuel use (Denman *et al.* 2007). The size of the flux is poorly quantified, largely because the amount of tropical forest that is cut and burnt is difficult to quantify, the carbon stocks in a given area of forest vary considerably and the carbon stocks are poorly quantified in most areas (Lewis 2006). Best

estimates among studies range from 0.9 to 2.2 Pg C year⁻¹, with a central estimate from recent studies of 1.6 (95% CI, 0.5–2.7) Pg C year⁻¹ for the 1990s (Denman *et al.* 2007; Ramankutty *et al.* 2007).

The rate at which wood decomposes determines the structural complexity and turnover of resources in ecosystems. In a thorough review of the decomposition of coarse woody debris in temperate ecosystems, Harmon *et al.* (1986) showed that the half-life of dead wood depended on several environmental and species-specific factors, and varied between a few years to over a century. The same orders of magnitude were found in tropical forests (Chambers *et al.* 2000). The main pathways for breakdown of wood are fire, xylophagous creatures, microbes (fungi, bacteria) and photo damage, although dysfunction and decay can happen via viruses as well.

Secondary chemicals have evolved as deterrents to insect damage (Croteau *et al.* 2000), and they occur in larger concentrations in bark, the outer defensive layer of functional wood and phloem. In addition, high-density woods decompose slower than low-density woods (Fig. 7, see also Chambers *et al.* 2000). From the data used to construct Fig. 7, we found that decay rate and wood density were strongly correlated in angiosperms ($R^2 = 0.208$, $n = 768$, $P < 0.001$), but not in conifers ($R^2 = 0.020$, $n = 67$, $P = 0.249$). The physical structure of wood, in addition to the tissue density and chemical composition, should influence fungal movement within the plant, and reduce the spread of fungal infections (Choat *et al.* 2008). Greater overall allocation to fibres and less allocation to conduits and parenchyma should also make wood less vulnerable to fungal decay (Fengel & Wegner 1984).

What causes differences in decomposition has been less well studied. In a meta-analysis, Weedon *et al.* (2009) associated decomposition rates of 102 woody species with

chemical and anatomical wood traits. Across all species, they found that decomposition was faster in angiosperms than gymnosperms. Angiosperms had denser wood, bigger conduits, higher nitrogen and phosphorous content, lower lignin content and lignin to nitrogen ratios (Cowling & Merrill 1966). It is typically thought that less dense wood should decay more quickly, so the result that the less dense gymnosperms decay more slowly is surprising. Whether differences in decomposition between the two groups are due to chemical differences (e.g. the higher lignin or lower nitrogen and phosphorous in gymnosperms) or physical differences (e.g. shorter and narrower conduits in gymnosperms) remains unclear.

6. SYNTHESIS AND FRONTIERS

Our review of wood traits, their interrelations and correlations with morphological, leaf and demographic traits and associated biogeographical and biogeochemical implications suggest that the functional ecological significance of wood is high (Fig. 4). However, this first synthesis also highlights some serious data deficiencies, and associated analyses needed to accurately describe functional trade-offs in wood. Ecologists should contribute to such a research programme.

Perhaps the most important task is to develop an agreed list of traits (Table 1) for a representative geo-referenced sample of woody plants from the world's biomes and biogeographical realms. Along with existing online databases (E.A. Wheeler's InsideWood database <http://insidewood.lib.ncsu.edu/>, see Wheeler *et al.* 2007) our data compilations have made some progress in this respect, but much more data are needed. Indeed, we have not attempted to construct a full matrix for the 20 or so traits listed in Table 1, because it would have been depressingly sparse. Among the most poorly documented are chemical traits in wood. To date these data have been confined to a specialized literature; however, it should be possible to compile datasets at a pace comparable to leaf chemistry datasets that have been assembled (e.g. Wright *et al.* 2004, 2007). The techniques of gathering N, P, K and Ca concentration from wood tissue are indeed now available in many laboratories across the world.

One important use of new information and an improved understanding of a well-defined wood economy spectrum would likely be in the development of more realistic dynamic global vegetation models (DGVMs). DGVMs model Earth's vegetation and its response to changing atmospheric conditions such as increasing atmospheric carbon dioxide concentrations and increasing air temperatures. These DGVMs show that forest dynamics could dramatically alter the response of the global climate system to increased atmospheric carbon dioxide over the 21st century with potentially serious societal and environmental

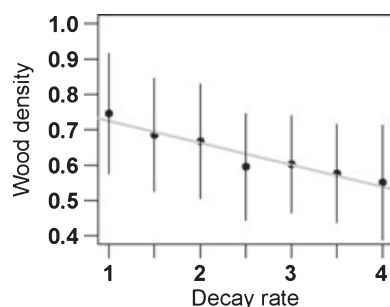


Figure 7 Relationship between wood density and mean wood decay rate classes (± 1 standard deviation, $n = 816$ species). Decay rate was scored on a scale from 1 to 4, with durable species being scored 1 and fast-decaying species being scored 4. Wood density data are from the wood database reported in the Appendix. Durability data are from Scheffer & Morrell (1998).

implications (Huntingford *et al.* 2008). However, there is little agreement among different DGVMs, making forest dynamics a major source of uncertainty in predicting future climate (Cramer *et al.* 2004).

Current DGVMs reduce complex forests to the total carbon stocks in various compartments – leaves, roots and trunks – with simple rules to determine how the carbon generated from photosynthesis is allocated to, and lost from, each compartment. Therefore, these models contain no information about wood. This absence is surprising as one of the key predictions of these models is the carbon storage per unit area at each time-step, essentially an estimate of the mass of wood, as > 90% of plant mass is woody.

The incorporation of wood traits in future DGVMs is likely to come from scaling up individual-based models of tree behaviour in forests (Marks & Lechowicz 2006) to regional and global scales (Purves & Pacala 2008). Allocation to wood is pivotal in such individual-based models, because they are based on competition for light, and individual plants invest in trunks to over-top others in a competitive struggle for light. Careful parameterization of global-scale individual-based models using data on patterns from a well-described wood economy spectrum may substantially reduce the uncertainty associated with current DGVMs. In turn, this would provide more robust predictions of future vegetation and climate as human activity alters the Earth system.

ACKNOWLEDGEMENTS

This contribution stems from a workshop held at the National Evolutionary Synthesis Center (NESCent), Durham, NC, USA, in 2007, co-funded by NESCent and ARC-NZ Research Network for Vegetation Function. This work was funded in part by a NESCent postdoctoral fellowship (NSF #EF-0423641) and NSF grant (#OISE-0502253) to A.E.Z. J.C. is supported by the ANR (ACI-Jeunes Chercheurs, and ANR-Biodiversité) and CNRS (programme AMAZONIE). S.L.L. is supported by a Royal Society University Research Fellowship. We gratefully acknowledge the help of G. Lopez-Gonzalez with the wood density database, and R.B. Miller, M. Wiemann and J. Ilic for sharing wood density data, and E. Wheeler for maintaining the InsideWood database, for useful conversations and for pointing us towards the durability dataset.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Glossary, Appendix, Figures S1–S2 and References.

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Editor, Johannes Knops

Manuscript received 15 October 2008

First decision made 12 November 2008

Manuscript accepted 12 January 2009