

Plant traits and wood fates across the globe: rotted, burned, or consumed?

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Abstract

Wood represents the defining feature of forest systems, and often the carbon in woody debris has a long residence time. Globally, coarse dead wood contains 36–72 Pg C, and understanding what controls the fate of this C is important for predicting C cycle responses to global change. The fate of a piece of wood may include one or more of the following: microbial decomposition, combustion, consumption by insects, and physical degradation. The probability of each fate is a function of both the abiotic environment and the wood traits of the species. The wood produced by different species varies substantially in chemical, micro- and macro-morphological traits; many of these characteristics of living species have ‘afterlife’ effects on the fate and turnover rate of dead wood. The colonization of dead wood by microbes and their activity depends on a large suite of wood chemical and anatomical traits, as well as whole-plant traits such as stem-diameter distributions. Fire consumption is driven by a slightly narrower range of traits with little dependence on wood anatomy. Wood turnover due to insects mainly depends on wood density and secondary chemistry. Physical degradation is a relatively minor loss pathway for most systems, which depends on wood chemistry and environmental conditions. We conclude that information about the traits of woody plants could be extremely useful for modeling and predicting rates of wood turnover across ecosystems. We demonstrate how this trait-based approach is currently limited by oversimplified treatment of dead wood pools in several leading global C models and by a lack of quantitative empirical data linking woody plant traits with the probability and rate of each turnover pathway. Explicitly including plant traits and woody debris pools in global vegetation climate models would improve predictions of wood turnover and its feedback to climate.

Keywords: C cycle, carbon, decomposition, fire, microbial decay, termites, wood

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Introduction

Trees and shrubs comprise a large fraction of the vegetation around the globe and have a profound effect

on the global carbon cycle (Bonan, 2008). Forests contain ~ 360 Pg C in plant biomass (Dixon *et al.*, 1994), with 10–20% of this amount present as coarse woody debris (CWD, Delaney *et al.*, 1998; Brown, 2002; Goodale *et al.*, 2002). However, depending on the ecosystem type and disturbance regime, this fraction may be much higher (Woldendorp *et al.*, 2004; Smithwick *et al.*, 2007). The

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residence time of C in CWD can be long (Mackensen *et al.*, 2003; Rock *et al.*, 2008; Weedon *et al.*, 2009). Although there is much published work on *in situ* wood decomposition rates in different biomes (Harmon *et al.*, 1986; Yin, 1999; Mackensen *et al.*, 2003; Rock *et al.*, 2008; Weedon *et al.*, 2009), the mechanisms that determine wood turnover rates and pool sizes are poorly characterized. It is thought that the rates depend on abiotic environmental conditions, woody species traits, and loss pathways; however, the individual and interactive influences of these effects especially outside temperate regions remain unclear. This uncertainty makes it difficult to predict how global changes in climate, disturbance regimes, and species composition will alter wood turnover.

A growing body of literature suggests that plant traits have predictable, long-term effects on ecosystem processes, especially 'afterlife' effects on litter decomposition (Hobbie, 1996; Allison & Vitousek, 2004; Cornelissen *et al.*, 2007; Cornwell *et al.*, 2008). Global changes can drive shifts in plant community composition that affect the distribution of plant functional traits (Suding *et al.*, 2008), and these shifts can generate feedbacks to global change (Chapin *et al.*, 2005; McGuire *et al.*, 2006; Cornelissen *et al.*, 2007). Although most trait-feedback studies have focused on plant leaves, wide variation in wood traits (Chave *et al.*, 2009) may also have important afterlife effects on turnover rate (Weedon *et al.*, 2009). Since dead wood is a major component of forest C budgets (Malhi *et al.*, 2004; Litton *et al.*, 2007), knowledge about the distribution and variation of wood traits is potentially valuable for predicting ecosystem responses to global change.

The goal of this paper is to review the major loss pathways for wood in ecosystems (Fig. 1), with an emphasis on the links between plant traits and wood fates. This effort is complementary to recent work on responses of decomposition to abiotic conditions (Parton *et al.*, 2007; Adair *et al.*, 2008) and an extension of recent work synthesizing global variation in wood traits (Swenson & Enquist, 2007; Chave *et al.*, 2009). We consider decomposition, insect consumption, fire, and physical degradation as the main loss pathways (Fig. 1), and attempt to summarize the effect of plant traits on the rate of wood turnover through each pathway. Correctly representing these wood fates, especially the balance between more-or-less steady decomposition rates vs. episodic combustion, is currently a crucial challenge in global vegetation-climate modeling (Cramer *et al.*, 2001). Therefore, we also make explicit recommendations for using plant traits to improve predictions of wood turnover in global vegetation-climate models.

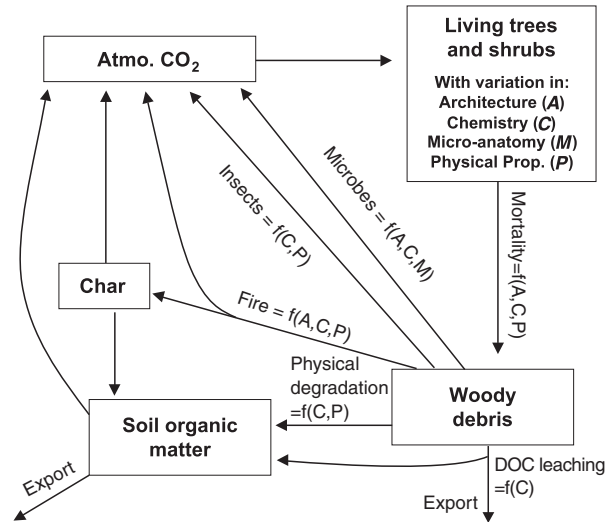


Fig. 1 The five major fates for woody debris are arrows from the woody debris pool. The probability of each pathway and the rate of transformation in that pathway are functions of both the abiotic environment (not explicitly shown in the diagram) and the various traits of the species (as indicated in the diagram). Note that both the mortality agents and wood fates depend on species wood traits, abiotic conditions, and biogeography and that interactions between pathways exist (see text). We only attempt to represent the trait effect here. We omit effects of traits on particular pathways when we could not find supporting evidence for the connection in the literature.

Wood fates

Microbial decomposition

Wood decomposition is thought to be controlled primarily by fungi, although the role of bacteria has not been explored extensively (Clausen, 1996). Wood-decomposing fungi are highly specialized in their foraging strategies (Boddy & Heilmann-Clausen, 2008) and are able to break down all components of wood including nonstructural compounds – sugars, lipids, and peptides – and structural compounds – hemicellulose, cellulose, and lignin. The rate of decomposition of wood by these fungi depends on the action of extracellular enzymes. In particular, lignin decomposition requires the production of oxidative enzymes that use either oxygen or peroxide to degrade the lignin polymer with free radical mechanisms (Kirk & Farrell, 1987; ten Have & Teunissen, 2001). Polysaccharides such as hemicellulose and cellulose are the other main constituent of wood, and microbes use specific enzymes to break down these polymers (Lynd *et al.*, 2002).

Different fungal species, including members of the Ascomycete, Basidiomycete, and Zygomycete fungal clades, are probably involved in various stages of wood decomposition (Dix & Webster, 1995). Some of these

taxa (especially the Zygomycetes) specialize on soluble sugars and other labile components of wood, while Basidiomycetes may be more important for degrading the polymers that dominate wood chemistry. Two groups of Basidiomycetes – the white rot and brown rot fungi – are well known for their wood-degrading capabilities. The white rot fungi are able to completely degrade all components of wood including lignin, while brown rot fungi attack the hemicellulose and cellulose components, leaving much of the lignin behind (Worrall *et al.*, 1997). One Ascomycete group – the Xylariaceae – cause a specific type of soft-rot that leads to the substantial disintegration of hard wood (including lignin) without the help of peroxidases (Liers *et al.*, 2006).

Consumption by invertebrates

There are many invertebrates that feed on dead wood, but it is likely that only termites and beetles have a significant global impact on wood decay. As a general rule, beetles are ecologically important only in particular ecosystems (e.g., deserts, montane ecosystems, very wet woodlands, coniferous forests) and microhabitats (e.g., very dry wood) (Crowson, 1981). Where termites and beetles co-exist, termites tend to be far more important wood consumers (Wood & Sands, 1978).

From a global C modeling perspective, we believe that termites deserve primary attention. All termites live in complex societies with a clear division of labor – almost all individuals function as workers, soldiers or reproductives. The workers feed directly on dead wood through a combination of mechanical shredding with their mandibles and digestion in their complex guts. In most termite species, digestion is predominantly mediated by microbes in the gut (Tokuda & Watanabe, 2007), some of which can fix N (Yamada *et al.*, 2006). However, the most efficient degraders of dead wood are in the Macrotermitinae. These termites construct in their nests a sheltered space for the growth of the mutualist white-rot fungus *Termitomyces* (Aanen & Eggleton, 2005), and this termite/fungal system can completely digest ligno-cellulose materials (Ohkuma, 2003).

Termites are not evenly distributed around the globe (Fig. 2b). Their highest diversities and abundances occur in tropical rain forests and tropical savannas, while they are largely absent from cold-temperate, boreal and polar regions (Eggleton, 2000). Termites probably affect wood turnover nearly everywhere they occur, but this effect is thought to be largest in tropical regions. Across tropical rain forests, there is large variation in termite diversity and density, with diversity declining as follows: Africa > South America > Asia > Madagascar > Australia (Davies *et al.*, 2003). The fun-

gus-growing termites of the Macrotermitinae are only found in Africa, Asia and Madagascar, and this biogeographical effect may be a critical determinant of termite impacts on wood turnover in different tropical regions (Schuurman, 2005).

Estimates of the proportion of wood that is consumed by termites in tropical forests are not well constrained, but this pathway is potentially of immense global importance. If we assume that termites mediate half of the wood decomposition in tropical forests (see references in Martius, 1994) and use recent estimates of woody NPP for tropical forests (Luyssaert *et al.*, 2007), we calculate that termites could be responsible for 1.9 Pg yr^{-1} of C flux to the atmosphere solely from tropical forests. There is likely to be a smaller, additional contribution from tropical savannas and subtropical and temperate forests. For example, in temperate forests of Tasmania, *Eucalyptus obliqua* logs lose 20–30% of their volume to termites (Stamm, 2006).

Fire

Annual C losses from vegetation due to fire are on the order of 4 Pg yr^{-1} and are dominated by products from C_3 plants in tree-dominated biomes (Fig. 2c), reflecting in large part the combustion of wood (Randerson *et al.*, 2005; Van de Werf *et al.*, 2006). Once shed as litter, wood becomes more vulnerable to burning in wildfires because of its position within reach of surface fires. During burning, wood may be consumed or converted to char, and these two processes compete with one another (Di Blasi, 1998; Drysdale, 1998). When the structural polymers that make up wood are heated, they can depolymerize to produce tars, which are then available for rapid combustion. Combustion releases wood C primarily as CO_2 . However, wildfires also produce small quantities of CO, methane, and elemental C aerosols as well as a complex mixture of organic compounds (Pak *et al.*, 2003; Preston & Schmidt, 2006).

In addition to the release of wood C to the atmosphere, fire converts some of the remaining solid mass to char, which oxidizes slowly. Char exhibits slower decomposition times than wood but is subject to slow weathering processes and downward or lateral transport in soils (Preston & Schmidt, 2006), but see Bird *et al.* (1999). In the only study (known to us) of char production from CWD following a wildfire (Tinker & Knight, 2000), the conversion rate of biomass C to charcoal in a *Pinus contorta* forest in Wyoming, USA amounted to 8%. An equal mass of C was consumed by the fire and released as gases and aerosols.

Circumstances that favor the charring reactions will both reduce the amount of biomass that a fire front immediately consumes and promote the formation of a

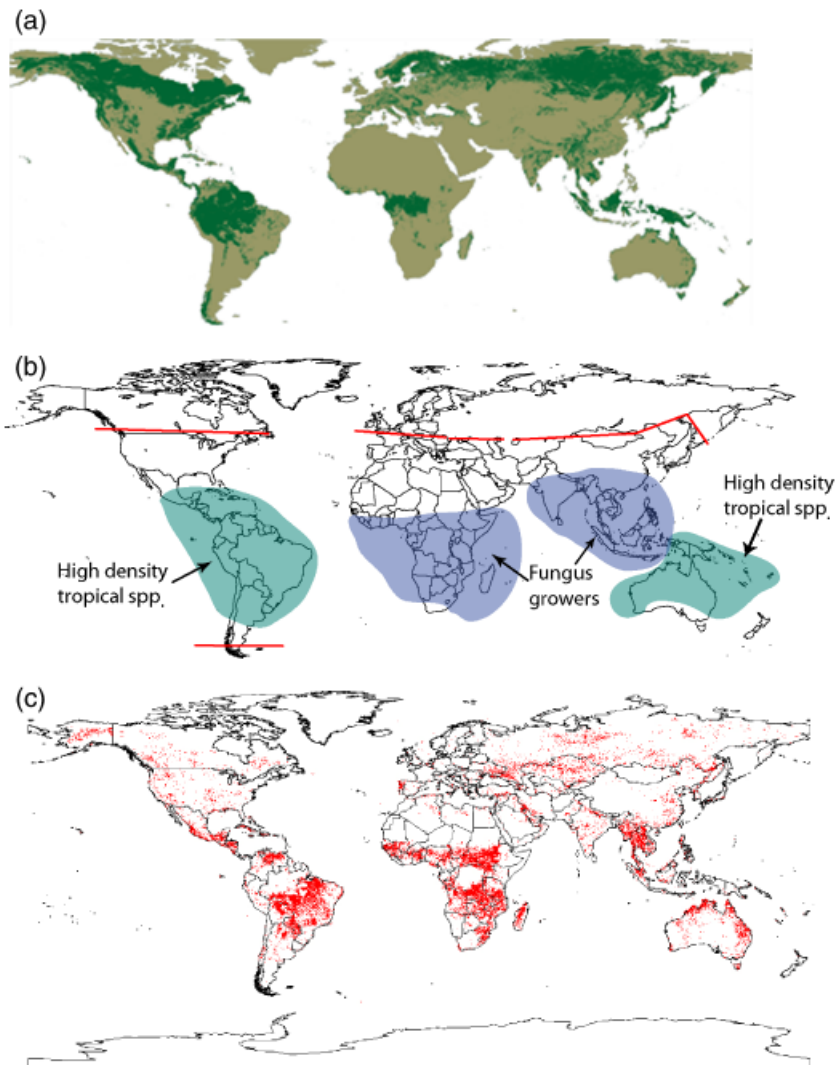


Fig. 2 Global distribution maps of (a) the current geographical extent of forests (Bryant *et al.*, 1997), (b) termites (Eggleton, 2000) with red lines representing the cutoff points beyond which no termites are found; areas with fungus growing termites are in blue; and nonfungus-growing termites in green, and (c) fires in 2005 (via satellite infra-red sensing by the European Space Agency) with each red point representing a separate fire.

residue of unoxidized charred material. However, the formation and oxidation of char both release heat, and these two reactions can allow fuels to continue to smolder after the main flame front has passed (Milošavljević *et al.*, 1996; Drysdale, 1998). This smoldering phase, which is particularly pronounced in very decayed wood, can lead to partial or complete consumption of the remaining material. Carbon emissions from the smoldering phase contain less CO₂ and more CO and methane (Ward *et al.*, 1992). Moderate fire temperatures, slow heating rates, and high lignin content in the fuel all favor charring (Drysdale, 1998; Antal & Grønli, 2003; Gundale & DeLuca, 2006). High moisture content shifts the balance of combustion chemistry towards charring, both by holding temperatures down and by

directly catalyzing charring reactions (Antal & Varhegyi, 1995).

Physical degradation

Photodegradation, leaching and physical damage (erosion and fragmentation) all contribute to the breakdown of woody material, either directly through physical export or indirectly by facilitating biological decomposition. UV light striking lignin-rich organic matter can create highly reactive free radicals, a process called photodegradation (Zabel & Morrell, 1992; Austin & Vivanco, 2006; Henry *et al.*, 2008). These radicals convert surrounding cell-wall constituents into soluble forms, which can be subsequently leached out of the wood.

The effects of UV may be of relative importance in dry biomes with high irradiance, such as (semi-) deserts, but the total wood C pool in such unproductive environments may be too low to be of global significance.

Removal of soluble material by water (leaching) is an important pathway of mass loss from leaf litter (Hagedorn & Machwitz, 2007) and is likely to also be important for woody litter (Spears & Lajtha, 2004). Leaching removes dissolved organic matter from decomposing plant material, both the original constituents and the products of degradation by microbes or other abiotic forces (Qualls & Haines, 1991). Therefore, while leaching may not make a large contribution to mass loss from wood on its own, it is the essential process in transporting transformed woody material either into soil C pools with fast turn-over times, into long-residence-time soil C pools, or out of the system (i.e., into the watershed). One detailed study of *Fagus sylvatica* logs showed that dissolved organic C was leached from logs into the topsoil underneath, but this did not lead to higher soil organic C (Kahl, 2008), suggesting that the extra C entering the soil can be respired quickly.

Plant traits – variation among wood types worldwide

Woody plant stems must balance several important functions for the living plant – long-distance transport of resources, mechanical support, and resource storage. Species vary in the chemical, physical, and anatomical traits that contribute to these functions, and we hypothesize that these traits have significant afterlife effects on pathways and rates of wood mass loss (Fig. 1). From the outside moving inside, woody plant stems consist of bark, vascular cambium, xylem, and pith. By far the largest pool of C in woody debris functioned as xylem in the living plant.

Below we summarize the important micro- and macro-morphological and chemical features of xylem and other wood tissues, with an emphasis on variation

among species. Intraspecific variation in wood traits exists (Maherali & DeLucia, 2000; Cornwell *et al.*, 2007). However, intraspecific variation only represents a small portion of trait shifts across different habitats (Cornwell & Ackerly, 2009). As such, we focus on among species-based variation in wood traits. We discuss the implications of these wood traits, and relevant whole-plant traits for the ultimate fate of wood C.

Chemical properties of stems

The chemical properties of wood – both the chemical composition and relative quantities of different constituents – determine the substrate quality for microbial decomposers and other pathways of C loss. While wood chemistry has been examined in a number of case studies, there has been no effort to collate or synthesize these data. To examine the importance of chemical differences, we conducted a novel literature synthesis in which we analyzed 71 papers with wood macronutrient and/or secondary chemistry data covering 146 species of dicot (eudicot, magnoliid and basal dicot) angiosperms and 53 gymnosperms (see Supporting Information for methods and references). We will use this synthesis to describe patterns throughout this section. Very little is known about wood chemistry in the pseudo-woody clades – tree ferns, palms, and bamboos. Therefore, we focus below on the main differences in wood chemistry between angiosperms (excluding monocots) and gymnosperms (Table 1), and implications of these differences for the composition and activity rates of microbes.

One of the defining properties of virtually all wood types is extremely high C:nutrient ratios (Sjöström, 1993), which makes nutrient limitation a serious constraint on wood decomposition. This constraint is probably most important in gymnosperm wood. Compared with angiosperm wood, gymnosperm wood has lower N, K, and Ca concentrations (Table 1). Not surprisingly,

Table 1 Results of meta-analysis of papers with published values for wood chemistry

	Units	Angiosperms			Gymnosperm				
		# of Spp.	Minimum	Median	Maximum	# of Spp.	Minimum	Median	Maximum
Lignin	%	103	14	26.2	38	34	23.3	29.3	38.5
Cellulose and glucose	%	88	32.5	46.2	79	31	33.0	44.1	56.2
Other sugars	%	64	10.6	20.8	36.6	15	17.6	23.3	33.2
Extractives	%	82	0.4	4.6	20.9	29	1.1	6.4	23.3
N	g kg ⁻¹	61	0.5	3.0	13.5	31	0.5	1.2	5.0
P	mg kg ⁻¹	61	22	234	1500	30	60	289	933
K	mg kg ⁻¹	55	29	1267	12000	30	160	675	4533
Ca	mg kg ⁻¹	53	270	2225	9200	28	400	1477	4800

For methods and references collated in this analysis, see Supporting Information.

there is good evidence that wood decomposition rates are positively correlated with wood nutrient concentrations, particularly nitrogen (Weedon *et al.*, 2009). Nitrogen is expected to limit decomposition because the degradative enzymes needed for wood decay are nitrogen-rich, with C:N ratios of $\sim 3:1$ (Serner & Elser, 2002), far narrower than wood ratios of 200–1200:1. As a result, the immobilization and accumulation of nitrogen during the decomposition process (Busse, 1994), the fixation of atmospheric N (Jurgensen *et al.*, 1984), the capture of N from atmospheric deposition (Kuehne *et al.*, 2008), and possibly the retranslocation of N through extensive fungal hyphae are important processes to reduce N limitation of fungi and accelerate wood decomposition. The retranslocation of N and other nutrients through fungal hyphae from soil or forest floor to logs has been often discussed (e.g., Wells & Boddy, 1995), but has not been systematically quantified.

Wood is primarily composed of carbohydrates (the β -linked polymer cellulose and a variety of hemicelluloses) and lignin, plus smaller amounts of secondary chemicals, including resins and tannins (Sjöström, 1993). Lignin is a complex three-dimensional structure based on phenylpropane monomer units, which are linked via ether or C–C bonds (Kirk & Farrell, 1987). Gymnosperm woods contain almost exclusively guaiacyl lignin based on coniferyl alcohol with one methoxyl group, whereas angiosperms also contain syringyl lignin derived from sinapyl alcohol with two methoxyls. Some gymnosperms have small traces of syringyl structures. All groups, but especially monocots, also contain small amounts of *p*-hydroxyphenyl lignin with no methoxyl groups (Hedges *et al.*, 1985; Logan & Thomas, 1985; Balakshin *et al.*, 2005). Guaiacyl lignin is typically more resistant to microbial decomposition than syringyl lignin, as suggested by a variety of techniques, especially analysis of specific lignin monomers released by CuO oxidation of soil and plant materials (Hedges *et al.*, 1985; Preston *et al.*, 1998; Martinez *et al.*, 2005). While our literature survey found similar median lignin levels for angiosperms (26.2%) and gymnosperms (29.3%), it is worth noting that not one gymnosperm species had <23% lignin in its wood. In contrast, 32% of angiosperm species (33 species out of 103) showed <23% lignin.

Our literature survey showed that extractives – non-structural secondary compounds – varied over 50-fold among angiosperm species and 20-fold among gymnosperm species (Table 1). Woods known for their durability are generally high in secondary compounds deposited in heartwood that can inhibit microbial decomposers through direct toxicity (Scheffer & Cowling, 1966). For example, xanthonenes from heartwood of the tropical tree *Calophyllum brasiliensis* inhibit the growth of brown rot fungi (Reyes-Chilpa *et al.*, 1997). Moreover,

termites generally avoid dead wood with large amounts of secondary plant chemicals (e.g., quinones, flavinoids, and terpenoids) (Scheffrahn, 1991; Watanabe *et al.*, 2005). There are also abundant gymnosperm species (e.g., the North American trees *Thuja plicata* and *Callitropsis nootkatensis*) in which decomposition is strongly limited by secondary compounds (Hennon *et al.*, 2007). Antifungal properties of some wood secondary compounds may be due to their antioxidant properties, which enhance the biocidal effects of other secondary compounds by reducing the effectiveness of fungal oxidative enzymes (Schultz & Nicholas, 2000).

Tannins could play an important role in wood decay. Only condensed tannins occur in gymnosperms, whereas angiosperms may contain both condensed and hydrolyzable tannins (Hernes & Hedges, 2004). Gymnosperms are also thought to be higher in alkyl C, reflecting higher resin content (Rowell, 2005). The differences in secondary chemistry and macronutrients between angiosperms and gymnosperms, the absence of low-lignin wood among gymnosperms, as well as the inherently greater resistance of guaiacyl lignin to decay may together partly explain why gymnosperm wood on average decomposes more slowly than angiosperm wood under similar environmental conditions (Weedon *et al.*, 2009).

Wood chemical traits can also affect flammability because structural polymers differ in their effects on both the combustion chemistry and water-holding capacity of wood. Tissues rich in lignin and extractives (e.g., heartwood) have reduced water storage capacity (Berry & Roderick, 2005). This could increase fuel consumption, particularly in environments with humid fire seasons. However, high-lignin woods may show less mass loss during fire because lignin has a high volatilization temperature and a strong tendency to char. In contrast, the tendency for tar formation and flaming is stronger in cellulose and still more so in hemicellulose (Di Blasi, 1998). Wood resins contribute to a modest increase in the heat content of wood (Bowyer *et al.*, 2007), but more importantly can be relatively volatile, allowing more rapid ignition in the flaming phase.

Although tannins and lignins inhibit microbial decomposition, these compounds may accelerate photo-degradative mass loss (Day *et al.*, 2007). This mass loss will usually be small in absolute terms, but nonetheless can be significant for biogeochemical cycling within dry, high-irradiance environments where biological degradation is especially slow (Austin & Vivanco, 2006).

Fine-scale anatomical traits

Water-conducting cells represent a major anatomical component of wood structure, and vary substantially

Table 2 Stem anatomy differences across woody and pseudo-woody plant clades

	Water transport cells		Support cells	Pit type	Wood density
	Water conduit type	Tissue type and cell arrangement			
Ferns (tree ferns)	Tracheids and vessels	Vascular bundles, either in a central stele region or central region with gaps for the vascular branches leading to fronds	Highly lignified sclerenchyma in bands around vascular bundles with a second thicker band external to the vascular tissue	Homogeneous pit membrane with pit dimorphism and high variation in pit porosity*	
Extant Gymnosperms	Tracheids†	Secondary xylem	Tracheids‡	Mainly torus/margo§; vestured pits in <i>Gnetum</i> and <i>Ephedra</i>	Typically low wood density
Monocots (palms, bamboo)¶	Tracheids and vessels	Scattered vascular bundles	Fibers and tracheids associated with bundles	Homogeneous, scalariform and sometimes opposite.	
Basal Angiosperms, Magnoliids, Eudicots	Mainly vessels**	Secondary xylem	Fibers and sometimes tracheids	Diverse but typically homogeneous; vestured pits characteristic of particular families	Highly variable wood density

*A torus has been illustrated in *Botrychium*.

†Except in the Gnetales, which have vessels.

‡Except in Gnetales, which have both fiber tracheids and tracheids.

§Except in the Cycadales, some Podocarpaceae, and some species in the Gnetales and Welwitschiaceae having homogenous pits. Tori are found in *Ephedra* and some species of *Gnetum*.

¶In botanical nomenclature, the 'wood' of palms and bamboos is termed 'anomalous' secondary growth.

||Some evidence of very porous membranes in end walls of tracheary elements.

**Except in the few basal groups that lack vessels, having wood composed of mostly tracheids (homoxylous). Species with similar vessel sizes across the growth ring are diffuse-porous and those with decreasing vessel sizes across the growth ring are ring porous. Gymnosperms, magnoliids, and eudicots are clearly the most important groups globally. However, bamboos and palms (Monocots), as well as tree ferns can be dominant locally and have important effects on ecosystems.

Bauch *et al.* (1972); Carlquist (1996); Morrow & Dute (1998); Carlquist and Schneider (2001); Stevens (2001–); Tyree and Zimmermann (2002); Large and Braggins (2004); Carlquist and Schneider (2006); Sperry *et al.* (2006).

among plant species and major clades (Table 2, Fig. 3) with potential implications for microbial decomposition. There is no evidence that fine-scale anatomy influences physical degradation or insect consumption (see Fig. 1). There is a complex relationship between fine-scale anatomy and wood density (Preston *et al.*, 2006b; Chave *et al.*, 2009) with implications for fire (discussed below).

Water-conducting cells comprise a large fraction of the xylem, have secondary walls reinforced with structural compounds, and lack protoplasts when mature. The relative abundance of conducting cells differs among the major clades of woody plants – 90 to 95% of cross-sectional area in gymnosperm wood is com-

prised of conducting cells, compared with only 3–55% in angiosperm wood (Fengel & Wegener, 1984; McCulloh & Sperry, 2005). One important class of conducting cells are tracheids, which have long thin cells with tapered ends and also provide mechanical support. On average, tracheids are 7–65 µm in diameter (Fengel & Wegener, 1984; Carlquist, 2001; Evert & Esau, 2007). The second major class of conduits is vessels, which are typically larger, with diameters of 5–400 µm (Fengel & Wegener, 1984; Carlquist, 2001; Evert & Esau, 2007). The diameter range for fungal hyphae is 0.5–20 µm with most in the range of 2–5 µm (Baath & Soderstrom, 1979; Zabel & Morrell, 1992). Therefore, all but the largest hyphae can move through most vascular conduits.

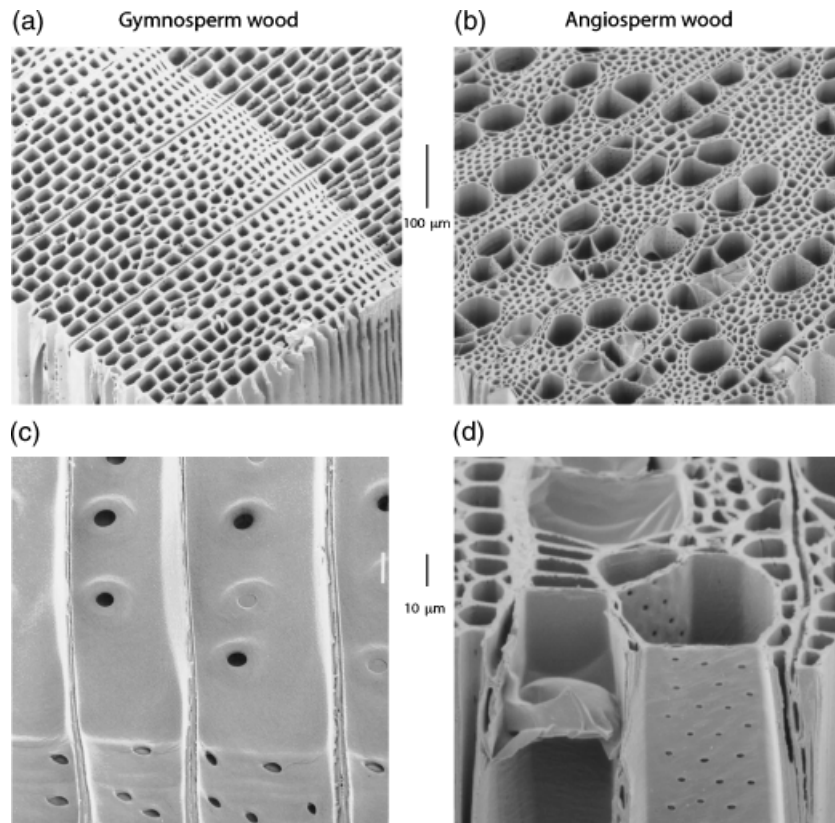


Fig. 3 Scanning electron microscope images of gymnosperm [*Abies* sp. (a) and (c)] and angiosperm [*Populus* sp. (b) and (d)] wood. In the gymnosperm images, the conduits are tracheids; in the angiosperm images, the largest conduits are vessels. During decomposition, fungal hyphae are small enough to grow through all types of vascular conduits (see text). However, the growth of large-diameter hyphae may be limited by the connections between conduits in both angiosperms and gymnosperms. These connections are termed 'pits' and are visible in panels (c) and (d). Note that the pits in (c) are torus/margo, with the torus only present in some pits. Also note that in general the mean length of conduits is shorter in gymnosperms compared with angiosperms, so growing hyphae will more frequently encounter interconduit connections in gymnosperm relative to angiosperm wood. See also Table 2 for more anatomical differences among clades of woody species. Photo credit: Japanese Wood Database.

The type of xylem conduit can have strong implications for decomposition. In gymnosperms, water transport occurs via single-celled tracheids. In angiosperms, most water transport occurs via vessels, which are a series of vessel elements (single cells) in which the ends of the cell wall are partially or fully digested, leaving perforation plates. The connection of the vessel elements via perforation plates leads to vessels of much greater lengths (up to 18 m) compared with tracheids (1–6 mm long; Carlquist, 2001). The large size of the apertures within perforation plates should not prevent fungi from moving between vessel elements.

The connections between tracheids and vessels may have relevance for microbial decomposition. These connections are made via *pits*, which are cavities in the cell wall with a water-permeable membrane formed of cellulose, hemicellulose, and pectins (see Fig. 3 and Choat *et al.*, 2008). Pits range from 3 to 12 µm in diameter in angiosperms and from 20 to 25 µm in

diameter in gymnosperms (S. Jansen pers. comm., Carlquist, 2001). In most species, pit openings are further restricted by a secondary cell wall extending over the pit that reduces the aperture to 30% of the total pit diameter (called 'bordered pits', S. Jansen pers. comm., Carlquist, 2001). Where pits occur and persist – the rate at which pits decay in dead wood is unknown – they are likely to restrict fungal colonization between conduits. The abundance of short tracheids, connected by pits, might explain the slower spread of fungal propagules in the functional wood of many gymnosperms compared with angiosperms (Boddy, 2001).

Fibers, rays, and parenchyma. Xylem also contains fibers and parenchyma. Fibers are the main support structures in angiosperms and provide storage for water and carbohydrates (Carlquist, 2001; Evert & Esau, 2007). Fibers have secondary walls and lack protoplasts when mature. They comprise 37–66% of the cross-

section (Fengel & Wegener, 1984). Parenchyma consists of the living cells in sapwood located axially or in rays. The proportion of wood cross-section that is parenchyma varies greatly across species: within angiosperms 11–30% of wood cross-sectional area can be rays and up to 11% axial parenchyma. Within gymnosperms, rays make up only 4–10% of cross-sectional area and most gymnosperms lack axial parenchyma (Fengel & Wegener, 1984; Evert & Esau, 2007).

When the proportion of parenchyma is high in sapwood (as in angiosperms), microbial decay should occur more quickly because this tissue type is richer in nitrogen and starch relative to other wood cell types (Evert & Esau, 2007; Weedon *et al.*, 2009). A higher fraction of parenchyma should also increase the amount of soluble compounds susceptible to leaching at the beginning of decomposition. There may also be relevant interactions between decomposability and the timing and mode of wood death. When functioning stems are broken from living plants, the plants are not able to resorb nutrients and carbohydrates before the stems are dropped (Milla *et al.*, 2005). The parenchyma in these stems should be more resource-rich than those in either senesced stems or heartwood.

Heartwood/Sapwood. The ratio of heartwood to sapwood in xylem may affect decomposition rates of trees or branches that have fallen or snapped while alive. Sapwood contains functional water-conducting cells, as well as living parenchyma, and heartwood contains nonfunctional xylem and dead parenchyma cells. In many species, the heartwood contains deposits of extractives (i.e., gums, tannins, and oils) and lower concentrations of N, P, and starch (Attiwill & Leeper, 1987). If active, the extractives can play an important role in slowing the decay of heartwood compared with sapwood as in North American *Quercus* spp. (Schowalter *et al.*, 1998). A few exceptional species – *Picea mariana* and *Abies alba* – notwithstanding, heartwood is also typically much drier than sapwood (Tyree & Zimmermann, 2002; Evert & Esau, 2007), which likely slows heartwood decomposition rates.

Physical properties of stems

Wood has evolved to function under an array of static and dynamic stresses from wind, water, ice, and snow (Romberger *et al.*, 2004). The ability of wood to function in the presence of such stresses is related to its mechanical properties. Mechanical properties are affected by the differences in tissue types and chemical composition, and these differences can lead to variation in wood basic density or specific gravity (Roderick & Berry, 2001). Wood densities range from 0.1 to 1.5 g cm⁻³

(Chave *et al.*, 2009), with denser wood tending to be mechanically stronger (van Gelder *et al.*, 2006). Wood density in gymnosperms is on average lower than in angiosperms, with a notable absence of gymnosperm species with very dense wood. At the same mean conduit size, angiosperms have fewer conduits per cross-sectional area (= less total cross-sectional area devoted to empty conducting cells) compared with gymnosperms, perhaps because, unlike gymnosperms, angiosperms do not rely on conducting cells for mechanical strength (Sperry *et al.*, 2008). In addition to other factors, mechanical strength will determine the degree to which stems and crowns shatter upon tree fall. This has implications for fragmentation and associated colonization (as discussed above) and the degree of soil contact.

Wood density has strong implications for consumption by termites, which avoid high-density hardwoods where possible (Arango *et al.*, 2006), and preferentially attack low-density, fast-growing tree species with low levels of defensive chemicals (Bultman & Southwell, 1976). Where termites can masticate the wood, they generally break down woody debris faster than fungi, but may be able to break down only a narrower range of wood densities, at least in the initial stages of decay. For example, a 13-yr experiment across a range of wood densities in Panama compared rates of wood turnover by fungi and termites. The termites outcompeted fungi, and possibly suppressed their decay rates, in the earliest decay periods and in the softest woods (Bultman & Southwell, 1976). Other estimates of termite effects from natural exclusion experiments do show similar patterns (Harmon *et al.*, 1995; Songwe *et al.*, 1995; Takamura & Kirton, 1999), but the data are too limited to draw definitive conclusions.

The density of wood also influences wood fate in wildfires. In living plants, denser wood has lower water content (Meinzer *et al.*, 2003; Sperry *et al.*, 2008), and this pattern likely carries over to dead wood that serves as fuel for fires. The influence of wood density on combustion chemistry is uncertain. Historically, dense woods have been understood to char more, consistent with their reputation as slow-burning firewoods. However, recent experiments associated with industrial charcoal production have found no relationship between wood density and char production (Antal & Grønli, 2003). In a mechanistic model of log smoldering, dense woods were predicted to smolder more in the wake of a wildfire (de Souza Costa & Sandberg, 2004).

Plant architecture

Surface area : volume. In contrast to other plant materials, especially leaves and fine roots, wood often has a low

surface area to volume ratio (SA:V). As such, access to the substrate can be an important limiting factor for decomposition. Log size is known to have a negative effect on decomposition rates (Mackensen *et al.*, 2003; Janisch *et al.*, 2005). The large diameter of some woody debris may also eventually limit the availability of N, O, and/or Mn, which are required by microbial decomposers (Preston *et al.*, 1998).

Any physical property of the wood that enhances either proportional surface area available for decomposer colonization or access to the interior of the wood substrate can have a dramatic positive effect on decomposition rates and subsequent material flux via leaching (Harmon *et al.*, 1986). In addition, wood that is more likely to splinter or shatter on its way to the soil surface will likely show faster decay rates. The degree to which a falling tree breaks into fragments depends on its mechanical wood properties, such as the arrangement of structural fibers (Kollmann & Cote, 1984). These effects appear to be more important than predecay wood density, which does not have a consistent effect on the decay rates of different species (Chambers *et al.*, 2000; Weedon *et al.*, 2009).

Plant architectural traits can have dramatic impacts on the consumption of woody litter in fires because they determine distribution of fuel sizes. Since the combustion of wood proceeds from the surface inward, the proportion of material converted during flaming is proportional to SA:V of the fuel (Rothermel, 1983). Also, thick wood pieces dry slowly and do not continue to burn after the surrounding environment cools (Drysdale, 1998). Therefore, species that allocate more photosynthate to thinner branches will produce wood that tends to be more completely consumed. After the flame front has passed, fuels can continue to smolder, resulting in the consumption of additional material. Smoldering can be responsible for the majority of biomass consumption in larger fuels because they are well insulated (Ward *et al.*, 1992).

Whole-plant morphology. A suite of traits related to plant architecture can affect wood losses by determining the degree of dead wood-soil contact following plant death. Plants with canopy structures that limit soil-wood contact after death, especially by forming snags (Garber *et al.*, 2005; Wilson & McComb, 2005), will be associated with reduced wood decay rates (van der Wal *et al.*, 2007). Plants with taller and more slender stems (i.e., a greater height:diameter ratio) have a larger proportion of mass away from the stem base and are therefore more likely to break under wind forces (Nishimura, 2005), depositing broken stems onto the ground. However, ultimately the degree of soil-wood contact will be a result of complex interactions between

plant traits (e.g., canopy types), stand structure, and disturbance regime.

Traits that increase the conversion of standing snags to downed wood bring fuels within reach of surface fires. In ecosystems that can experience severe fire conditions, retention of dead branches increases fire intensity by presenting dry fuels in a well-aerated structure where high fire temperatures are maintained by cross-radiation between burning limbs, leading to crown fires (Drysdale, 1998; Schwilk, 2003). For the same reason, finely branched live canopy structures increase fire intensity, and therefore fuel consumption, in crown fire-prone forests and shrublands.

Bark traits

The inner bark contains phloem, and the outer bark contains phellem (cork cells), phellogen (cork cambium), and phelloderm (cork skin with living cells sometimes highly sclerified or lignified) (Sandved *et al.*, 1993; Vaucher & Eckenwalder, 2003; Romberger *et al.*, 2004; Evert & Esau, 2007). Bark can also contain resins, latex, tannins, and other substances toxic to insects and fungi (Sandved *et al.*, 1993). The outer bark, especially the suberized cork, protects the stem while the inner bark transports sugars and amino acids (Sandved *et al.*, 1993; Vaucher & Eckenwalder, 2003; Romberger *et al.*, 2004). Bark thickness can range from 1 mm to tens of centimeters.

The type and thickness of bark will affect both microbial access to the xylem and the microclimate inside the decaying material. In living trees, one function of bark is to repel insects, fungi, and other pathogens, and this function is likely maintained for some time after the plant dies. Therefore, thick and resistant bark could limit microbial access to the wood substrate during the initial phases of decomposition. However, bark could ultimately have a positive effect on decomposition rates if it helps to moderate the microclimate within the wood, for instance by increasing moisture retention. This might be the case in northern birches (*Betula* spp.), in which the shape and tissues of the bark are often still relatively intact while the xylem inside has decayed. To our knowledge, no studies have examined the effect of bark removal on wood decay rates.

Bark thickness is a strong correlate of fire survival in live trees (Gill, 1995; Barlow *et al.*, 2003) and presumably thicker bark has the same protective effect for downed wood. Limited data suggest that bark has a greater tendency to char due to its acidity and high content of lignin, tannins, and ash (Richards & Zheng, 1991; Johnson, 1992; Kandola *et al.*, 1996; Bisanda *et al.*, 2003; Bowyer *et al.*, 2007). However bark from some species (e.g., some *Eucalyptus* sp.) is highly flammable, reflect-

ing a loose dry structure or the presence of resins (Barlow *et al.*, 2003). Bark also slows wetting and drying times of dead wood and appears to influence the burn time of dead wood most when the wood is not fully dry (Albini & Reinhardt, 1995; Defo & Brunette, 2006).

Root traits

Fully exploring belowground decomposition processes is beyond our scope (for a full treatment see Gill & Jackson, 2000). Here, we briefly consider the effect of root trait variation among species on the fate of aboveground wood.

Belowground plant traits including the strength, depth, and extent of root systems vary greatly among species (Jackson *et al.*, 2007) and can affect the rate at which dead wood comes in contact with the soil. In extreme cases, roots can grow as deep as 100 m and tap-rooted species may have large-diameter roots down to a depth of 20 m (Canham *et al.*, 2001; Peterson, 2007). These traits can affect the disturbance regime (further discussion below) and the fate of aboveground wood. After death, the structural integrity of root systems can last for many years (Polomski & Kuhn, 2001; Martin & Ogden, 2006). This is in part due to high suberin, tannin, and lignin content in the outer bark (Preston *et al.*, 2006a; Jackson *et al.*, 2007) and in part because both microbial biomass (Fierer *et al.*, 2003) and the oxygen to support high fire temperature decline with soil depth.

Trait effects on mode of plant death and exposure to decomposition

In some ecosystems, plant traits may drive or interact with disturbance regimes to influence the mode of plant death. The way a plant dies may then have strong implications for the fate of its wood. For example, ecosystems dominated by plants with fire-promoting traits (e.g., dead branch retention in *Adenostoma fasciculatum* in California) will likely show larger wood losses due to high-temperature, intense crown fires (Schwilk & Ackerly, 2001; Schwilk, 2003). Tall evergreen and shallow rooted trees are more likely to be windthrown in areas susceptible to storms (Schutz *et al.*, 2006).

Plant traits may also influence susceptibility to other types of disturbance with differing implications for post-mortem decomposition. Some mortality agents (e.g., wind or elephants) cause the immediate transfer of all or part of the woody material to the forest floor. In contrast, plant traits and mortality pathways leading to standing dead wood such as caused by pathogens or pest species may substantially slow subsequent decomposition because of low wood moisture content found in standing dead wood (Everett *et al.*, 2000; Runkle,

2000; Wilson & McComb, 2005). Insect outbreaks and fires often leave the trees upright, except in permafrost systems, where high intensity fires may destroy the rooting substrate by consumption of the organic layer (Yarmishko & Dem'yanov, 1983; Kajimoto *et al.*, 2003).

There are also important trait-driven interactions among the loss pathways. Organisms that attack dead wood can alter both the chemistry and the size distribution of fuels. It has been proposed that decay lowers the temperature at which dead wood ignites (Albini & Reinhardt, 1997), which would be consistent with decomposers preferentially breaking down certain less flammable substrates. Certainly the hollowing out of downed logs or standing snags by termites or microbes creates ideal conditions both for intensified flaming and sustained smoldering in the wake of a wildfire. Conversely, fire damage can also facilitate colonization by fungi and allow subsequent invasion by termites or beetles (Gill, 1995).

Representing the fate of dead wood in models

Here, we assess how dead wood dynamics are currently represented in global models, and the potential for models to incorporate factors affecting wood turnover, in particular, plant traits. We focus on three key factors controlling wood turnover: (1) wood traits affecting microbial decomposition, (2) positioning of dead wood in the ecosystem, and (3) alternate loss pathways such as fire and termites. In our discussion, we consider three global dynamic vegetation models: LPJ (Sitch *et al.*, 2003), LM3V (Shevliakova *et al.*, in press), and TEM (McGuire *et al.*, 1992; Euskirchen *et al.*, in press). We also evaluate two biogeochemical models: CENTURY (Parton *et al.*, 1988) and Biome-BGC (Running & Gower, 1991; Thornton, 1998) (Table 3). CENTURY itself has not been used for global applications, but its components have been used in ORCHIDEE (Krinner *et al.*, 2005) and the ED model (Moorcroft *et al.*, 2001), both of which are used to model the terrestrial biosphere in state-of-the-art earth system models.

Models generally represent plant functional diversity using a variable number of plant functional types (PFTs, see Table 3), which typically include a distinction between angiosperm and gymnosperm trees. Computational considerations have limited the number of PFTs to four in LM3V and to eight in LPJ. In CENTURY PFTs are user-defined, which is also true for the gap-version of LPJ (Smith *et al.*, 2001).

We divide models into two categories based on their complexity in representation of dead wood dynamics. In 'non-explicit' models, such as TEM, LPJ, and LM3V, wood is incorporated immediately into generic soil C pools as opposed to a separate woody debris pool.

Table 3 Overview of woody debris dynamics in selected ecosystem models with global application

	LPJ	LM3V	TEM ¹	CENTURY	Biome-BGC
<i>Process representation</i>					
Type	type-1	type-1	type-1	type-2	type-2
Separate woody debris compartment	n	n	n	y (BR,CWD,CR)	y
Baseline decay rate	0.35 yr ⁻¹ at 10 °C	80%–0.06 yr ⁻¹	ud	ud	?
		20%–10 yr ⁻¹			
Compound specific	n	n	n	y (structural, metabolic)	n
Woody-debris-specific moisture	y	n	n	n	n
Woody-debris-specific temperature	n	n	n	n	n
<i>Diversity representation</i>					
Number of woody PFTs	8	4	ud	ud	5
Separate angiosperm/gymnosperm	y	y	y	y	y
<i>Wood characteristics</i>					
Wood density	n	y	n	n	n
Bark thickness	n	n	n	n	n
Sapwood/heartwood	y	y	?	y	y
Nitrogen	y	n	y	y	y
Phosphorus	n	n	n	y	n
Lignin concentration	n	n	n	y	y
Labile carbon	n	y	n	n	y
Secondary chemistry	n	n	n	n	n
Parenchyma	n	n	n	n	y
Conduit area/porosity type	n	n	n	n	n
Positioning effects	n	n	n	y (standing, lying)	n
<i>Dimension/positioning</i>					
Tree size	y-mean	y-mean	n	n	n
Log size	y-mean	y	n	n	n
Sizes of other woody components	n	n	n	n	n
<i>Dead wood production/disturbance</i>					
Fire	y	y	n	y	y
Wind	n	n	n	n	n
Background mortality	y	y	n	y	y
Fractional consumption by fire	n	n	n	y	y
Fire resistance	y	n	n	n	n
Lag phase	n	n	n	y	n

type-1, non-explicit; type-2, explicit; n, no; y, yes; ud, user defined; BR, branch; CR, coarse roots; CWD, coarse woody debris; T, temperature; M, moisture; PFT, plant functional type. For references see text.

LM3V distributes the material into a slow (80%) and a fast pool (20%). LPJ has a litter pool that combines leaf, root, and woody litter into a single compartment. The baseline decay rate of litter in LPJ is 0.35 yr⁻¹, which is 10 times faster than the typical decay rates for coniferous wood (Weedon *et al.*, 2009) and thus unrealistic if the litter compartment is assumed to reflect dead wood dynamics. Residual material is transferred to intermediate and slow pools. In the current version of TEM, no distinction is made between litter fractions and soil C pools. All organic material decomposes according to a PFT-specific decay rate modulated by temperature and moisture.

'Explicit' models like Biome-BGC and the forest submodel of CENTURY include a separate woody debris

pool. The material lost from this pool is either respired or transferred into different soil pools. In Biome-BGC, dead wood entering the forest floor is subject to a baseline fragmentation rate modified by soil temperature and moisture (Thornton, 1998). For a temperate climate with a growing season of about 6 months, the current parameterization results in decay rate of about 0.1 yr⁻¹, which is typical for woody debris of deciduous trees (Harmon *et al.*, 1996). The remaining C is transferred into different pools with turnover times dependent on the wood extractives, cellulose, and lignin. A very similar approach is taken by the YASSO model (Liski *et al.*, 2005). In the forest submodel of CENTURY, woody litter enters size-specific woody debris pools (CWD, fine branch litter, etc.) each with its own baseline

decay rate (again modified by temperature and moisture). The transfer to subsequent soil organic matter (SOM) pools is regulated via a lignin:N ratio.

Wood traits. Wood traits are used in two different ways to specify woody debris decay rates in models. In nonexplicit models, wood traits control the allocation of woody litter into SOM pools with different turnover times. For temperate and boreal ecosystems, the use of wood chemical composition, especially lignin:N ratio, as a criterion for dividing the material into pools with different decay rates seems to be a good approach. The relatively low decomposition rates of conifers and the relatively fast decay rates of deciduous broadleaved trees are likely related to (or at least correlated with) differences in C:N and lignin:N ratios (see section on wood chemical traits and Weedon *et al.*, 2009). This is fortuitous because all models, even those without an explicit N-cycle, use C:N ratios to predict respiration rates in living tissue.

In explicit models, wood traits are used to predict a baseline decay rate for the woody debris pool, which corresponds to CWD in nature. This approach is useful because the model can be parameterized with field observations, and species or group differences in decay rates can be incorporated directly (see Rock *et al.*, 2008). These model features are particularly advantageous when decay rates are influenced by characteristics other than lignin and N concentration such as secondary metabolites, starch concentration, or wood anatomical features (e.g., wood density, conduit type, or the fraction of living cells).

Positioning and size. So far, CENTURY is the only model that includes positioning effects. The dead wood enters an inert standing woody debris pool. After a lag-time, it is transferred to the 'main' woody debris pool where it starts to decay. Decomposition as standing dead wood is therefore not considered. During the decay process, wood moisture content is equated with soil moisture, which is probably a poor approximation (Harmon & Sexton, 1995). The size of logs is incorporated indirectly into CENTURY via pools referring to size classes. Changes in the sapwood/heartwood ratio are also implicitly included since separate pools represent sapwood and heartwood. However, log size *per se* does not exist as a separate state variable in CENTURY, Biome-BGC, TEM, or LM3V. LPJ represents tree populations via a 'mean-plant approach', meaning that trees do have a size and size-effects could be directly modeled.

Additional turnover agents. Woody debris losses aside from microbial decomposition are primarily due to consumption by termites or fire. Currently, none of

the models includes termites, although future analyses could subsume the termite impact into the temperature response of wood decomposition, since termites tend to occur at high density in warmer climates. However, this nonmechanistic approach could lead to poor predictions because of termite biogeography, especially the absence of the clade of most effective wood consumers – fungus-growers – in the neo-tropics.

Fire consumption is treated very simply in LPJ, TEM and LM3V. In LPJ both the biomass and the total litter pool is consumed. In LM3V there is no separate litter compartment and only the aboveground biomass is consumed. The current version of TEM does not include fire losses at all, but a fire module including fractional fire mortality and consumption of dead wood is currently under development (D. McGuire, pers. comm.). As of now, all these models fail to reproduce the important legacy effect of dead wood: living trees are rarely consumed entirely by fire in the real world, and forest ecosystems recovering from fire are usually C sources because of high respiratory losses from dead wood (Harmon *et al.*, 1996; Wirth *et al.*, 2002). Thus, models with complete combustion tend to overestimate fire losses and underestimate woody debris C storage. Biome-BGC and CENTURY allow for constant fractional C losses following fire, but do not consider fuel moisture effects on the completeness of combustion.

Knowing the quantity of char that is highly thermally transformed is particularly important since this material is highly resistant to decomposition (Preston & Schmidt, 2006). Wildfire models that explicitly represent the competitive processes of char and tar formation are available (Colman & Linn, 2003), but are too computationally expensive to be suitable for direct incorporation into global models. However, these kinds of physics- and chemistry-based models could be used to inform parameter values that control char production in global C models, based on fire intensity, fuel moisture and wood traits. The value of representing char in global C models will depend on how much C is diverted into this compartment, on which there is very little data. Examining the effect of a wildfire on CWD in a pine forest, Tinker & Knight (2000) found that char represented ~ 10% of the solid material remaining.

In summary, the five models vary considerably in the representation of processes relevant for woody debris dynamics. CENTURY includes the most detail, but when CENTURY has been incorporated into global models, the formulations specific for dead wood have not been used. Keeping in mind the need for simplicity in global models, we suggest the following: (1) Fire should not totally consume the wood of live trees to allow for the important legacy effect of dead wood decomposition, and (2) A separate woody debris

compartment should be used. This would enable the models to represent the known trait-based and PFT-specific differences in wood decay rates that are probably not sufficiently reflected by lignin:N ratios alone. Moreover, a separate aboveground dead wood compartment would facilitate the calculation of fire fuel availability and status as well as fuel consumption. Where woody debris is immediately channeled into soil pools, it cannot be available for combustion. A separate standing dead wood pool would also allow a distinction between fine and coarse fuels, which may differ dramatically in flammability depending on humidity.

Conclusions

Shifts in the distributions of woody species that are likely under global change may have important impacts on the global C cycle (Bonan, 2008). Woody plants vary substantially in their stem traits and architecture, and these differences can clearly affect the fate of woody debris in ecosystems. As plant species distributions, physiological processes, and the management of ecosystems respond to environmental change, we can expect plant traits to shift as well, leading to altered rates of wood turnover in many ecosystems. Therefore, a trait-based approach to wood turnover should improve our understanding and modeling of the C cycle under global change.

Although we conclude that woody plant traits will be useful for predicting C cycle responses to global change, additional research is needed to quantify the effect of traits on different turnover pathways. Wood turnover by microbes, termites, and fire is governed by interactions between stem traits and environmental conditions that remain poorly understood, particularly in tropical ecosystems. At least for microbial ecology, advances in gene expression and enzyme assay techniques offer an important opportunity to make progress in this direction. Also, in many ecosystems such as tropical forests, less sophisticated research approaches to study the dynamics and decomposition of woody debris can contribute greatly to address the information gaps. With respect to fire, there is much promise in connecting combustion models with specific chemical and architectural characteristics of wood, which are now becoming available in global datasets on plant traits. Greater efforts to understand the rate at which wood rots, burns, chars, gets eaten, or just sits there will greatly improve models and predictions of the C cycle under global change.

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References

- Aanen DK, Eggleton P (2005) Fungus-growing termites originated in African rain forest. *Current Biology*, **15**, 851–855.
- Adair EC, Parton WJ, Del Grosso SJ *et al.* (2008) Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. *Global Change Biology*, **14**, 2636–2660.
- Albini FA, Reinhardt ED (1995) Modeling ignition and burning rate of large woody fuels. *International Journal of Wildland Fire*, **5**, 81–91.
- Albini FA, Reinhardt ED (1997) Improved calibration of a large fuel burnout model. *International Journal of Wildland Fire*, **7**, 21–28.
- Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive species in Hawai'i. *Oecologia*, **141**, 612–619.
- Antal MJ, Varhegyi G (1995) Cellulose pyrolysis kinetics: the current state of knowledge. *Industrial and Engineering Chemistry Research*, **34**, 703–717.
- Antal MJ, Grønli M (2003) The art, science and technology of charcoal production. *Industrial Engineering and Chemistry Research*, **42**, 1619–1640.
- Arango RA, Green F, Hintz K, Lebow PK, Miller RB (2006) Natural durability of tropical and native woods against termite damage by *Reticulitermes flavipes* (Kollar). *International Biodeterioration & Biodegradation*, **57**, 146–150.
- Attiwill PM, Leeper GW (1987) *Forest Soils and Nutrient Cycles*. Melbourne University Press, Carlton, Victoria.
- Austin AT, Vivanco L (2006) Abiotic and biotic controls on litter decomposition in the semiarid Patagonian steppe. *Nature*, **442**, 555–558.
- Baath E, Soderstrom B (1979) Significance of hyphal diameter in calculation of fungal bio-volume. *Oikos*, **33**, 11–14.
- Balakshin MY, Capanema EA, Goldfarb B, Frampton J, Kadla JF (2005) NMR studies on Fraser fir *Abies fraseri* (Pursh) Poir. lignins. *Holzforschung*, **59**, 488–496.
- Barlow J, Lagan BO, Peres C (2003) Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology*, **19**, 291–299.
- Bauch JW, Liese W, Schultze R (1972) The morphological variability of the bordered pit membranes in gymnosperms. *Wood Science and Technology*, **6**, 165–184.
- Berry SL, Roderick ML (2005) Plant-water relations and the fibre saturation point. *New Phytologist*, **168**, 25–37.
- Bird MI, Moyo C, Veenendaal EM, Lloyd J, Frost P (1999) Stability of elemental carbon in a savanna soil. *Global Biogeochemical Cycles*, **13**, 923–932.

- Bisanda ETN, Ogola WO, Tesha JV (2003) Characterisation of tannin resin blends for particle board applications. *Cement and Concrete Composites*, **25**, 593–598.
- Boddy L (2001) Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. In: *Ecology of woody debris in boreal forests (Ecological Bulletins 49)* (eds Jonsson BG, Krus N), pp. 43–56. Lund.
- Boddy L, Heilmann-Clausen J (2008) Basidiomycete community development in temperate Angiosperm wood. In: *Ecology of Saprotrophic Basidiomycetes* (eds Boddy L, Frankland J, Van West P), pp. 211–238. Academic Press, London.
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449.
- Bowyer JL, Schmulsky R, Haygreen JG (2007) *Forest Products and Wood Science: An Introduction*. Blackwell, Oxford.
- Brown S (2002) Measuring carbon in forests: current status and future challenges. *Environmental Pollution*, **116**, 363–372.
- Bryant DG, Nielsen D, Tangle L, Forest Frontiers Initiative (World Resources Institute) (1997). *The last frontier forests : ecosystems and economies on the edge: what is the status of the world's remaining large, natural forest ecosystems?* World Resources Institute, Forest Frontiers Initiative, Washington, DC.
- Bultman J, Southwell C (1976) Natural resistance of tropical American woods to terrestrial wood-destroying organisms. *Biotropica*, **8**, 71–95.
- Busse MD (1994) Downed bole-wood decomposition in lodgepole pine forests of central Oregon. *Soil Science Society of America Journal*, **58**, 221–227.
- Canham CD, Papaik MJ, Latty EF (2001) Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research*, **31**, 1–10.
- Carlquist S (1996) Wood, bark, and stem anatomy of Gnetales: a summary. *International Journal of Plant Science, Supplement*, **157**, 58–76.
- Carlquist S, Schneider EL (2001) Vessels in ferns: structural, ecological, and evolutionary significance. *American Journal of Botany*, **88**, 1–13.
- Carlquist S, Schneider EL (2006) Origins and nature of vessels in monocotyledons. 8. Orchidaceae. *American Journal of Botany*, **93**, 963–971.
- Carlquist SJ (2001) *Comparative Wood Anatomy: Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood*, 2nd, completely revised edn. Springer, Berlin.
- Chambers JQ, Higuchi N, Schimel JP, Ferreira LV, Melack JM (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, **122**, 380–388.
- Chapin FS, Sturm M, Serreze MC *et al.* (2005) Role of land-surface changes in Arctic summer warming. *Science*, **310**, 657–660.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Choat B, Cobb AR, Jansen S (2008) Structure and function of bordered pits: new discoveries and impacts on whole-plant hydraulic function. *New Phytologist*, **177**, 608–625.
- Clausen CA (1996) Bacterial associations with decaying wood: a review. *International Biodeterioration & Biodegradation*, **37**, 101–107.
- Colman JJ, Linn RR (2003) Non-local chemistry implementation in HIGRAD/FIRETEC. In: *5th Symposium on Fire and Forest meteorology*. American Meteorological Society, Orlando, FL.
- Cornelissen JHC, van Bodegom PM, Aerts R *et al.* (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, **10**, 619–627.
- Cornwell WK, Ackerly DD (2009) Community assembly and shifts in the distribution of functional trait values across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.
- Cornwell WK, Bhaskar R, Sack L, Cordell S, Lurch CK (2007) Adjustment of structure and function of *Metrosideros polymorpha* at high versus low precipitation. *Functional Ecology*, **21**, 1063–1071.
- Cornwell WK, Cornelissen JHC, Amatangelo K *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.
- Cramer W, Bondeau A, Woodward FI *et al.* (2001) Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Crowson RA (1981) *The Biology of the Coleoptera*. Academic Press, London.
- Davies RG, Eggleton P, Jones DT, Gathorne-Hardy FJ, Hernandez LM (2003) Evolution of termite functional diversity: analysis and synthesis of local ecological and regional influences on local species richness. *Journal of Biogeography*, **30**, 847–877.
- Day TA, Zhang ET, Ruhland CT (2007) Exposure to solar UV-B radiation accelerates mass and lignin loss of *Larrea tridentata* litter in the Sonoran Desert. *Plant Ecology*, **193**, 185–194.
- de Souza Costa F, Sandberg D (2004) Mathematical model of a smouldering log. *Combustion and Flame*, **139**, 227–238.
- Defo M, Brunette G (2006) A log drying model and its application to the simulation of the impact of bark loss. *Forest Products Journal*, **62**, 71–77.
- Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica*, **30**, 2–11.
- Di Blasi C (1998) Comparison of semi-global mechanisms for primary pyrolysis of lignocellulosic fuels. *Journal of Analytical and Applied Pyrolysis*, **47**, 43–64.
- Dix NJ, Webster J (1995) *Fungal Ecology*. Chapman & Hill, London.
- Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.
- Drysdale D (1998) *An Introduction to Fire Dynamics*, 2nd edn. John Wiley & Sons, Brisbane.
- Eggleton P (2000) Global patterns of termite diversity. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (ed. Abe MhaDB T), pp. 25–52. Kluwer Academic, Dordrecht.
- Euskirchen E, McGuire A, Chapin F III, Yi S, Thompson C (in press) Changes in plant communities in Northern Alaska

- under scenarios of climate change 2003–2100: implications for climate feedback. *Ecological Applications*.
- Everett R, Lehmkuhl J, Schellhaas R, Ohlson P, Keenum D, Riesterer H, Spurbeck D (2000) Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. *International Journal of Wildland Fire*, **9**, 223–234.
- Evert RF, Esau K (2007) *Esau's Plant Anatomy: Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development*, 3rd edn. John Wiley, Hoboken, NJ.
- Fengel D, Wegener G (1984) *Wood: Chemistry, Ultrastructure, Reactions*. W. de Gruyter, Berlin.
- Fierer N, Schimel JP, Holden PA (2003) Variations in microbial community composition through two soil depth profiles. *Soil Biology & Biochemistry*, **35**, 167–176.
- Garber SM, Brown JP, Wilson DS, Maguire DA, Heath LS (2005) Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. *Canadian Journal of Forest Research*, **35**, 787–796.
- Gill AM (1995) Stems and fires. In: *Plant Stems: Physiology and Functional Morphology* (ed. Gartner BL), pp. 323–339. Academic Press, New York.
- Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, **147**, 13–31.
- Goodale CL, Apps MJ, Birdsey RA *et al.* (2002) Forest carbon sinks in the Northern Hemisphere. *Ecological Applications*, **12**, 891–899.
- Gundale MJ, DeLuca TH (2006) Temperature and source material influence ecological attributes of ponderosa pine and Douglas-fir charcoal. *Forest Ecology and Management*, **231**, 86–93.
- Hagedorn F, Machwitz M (2007) Controls on dissolved organic matter leaching from forest litter grown under elevated atmospheric CO₂. *Soil Biology and Biochemistry*, **39**, 1759–1769.
- Harmon ME, Franklin JF, Swanson FJ *et al.* (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **15**, 133–302.
- Harmon ME, Garman SL, Ferrell WK (1996) Modeling historical patterns of tree utilization in the Pacific Northwest: carbon sequestration implications. *Ecological Applications*, **6**, 641–652.
- Harmon ME, Sexton J (1995) Water-balance of conifer logs in early stages of decomposition. *Plant and Soil*, **172**, 141–152.
- Harmon ME, Whigham DF, Sexton J, Olmsted I (1995) Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. *Biotropica*, **27**, 305–316.
- Hedges JL, Cowie GL, Ertel JR, Barbour RJ, Hatcher PG (1985) Degradation of carbohydrates and lignins in buried woods. *Geochimica et Cosmochimica Acta*, **49**, 701–711.
- Hennon P, Woodward B, Lebow P (2007) Deterioration of wood from live and dead Alaska yellow-cedar in contact with soil. *Forest Products Journal*, **57**, 23–30.
- Henry HAL, Brizgys K, Field CB (2008) Litter decomposition in a California annual grassland: interactions between photodegradation and litter layer thickness. *Ecosystems*, **11**, 545–554.
- Hernes PJ, Hedges JI (2004) Tannin signatures of barks, needles, leaves, cones, and wood at the molecular level. *Geochimica et Cosmochimica Acta*, **68**, 1293–1307.
- Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503–522.
- Jackson RB, Pockman WT, Hoffmann WA, Bleby TM, Armas C (2007) Structure and function of root systems. In: *Functional Plant Ecology*, 2nd edn (eds Pugnair FI, Valladares F), pp. 151–174. CRC Press, Boca Raton, FL.
- Janisch JE, Harmon ME, Chen H, Fasth B, Sexton J (2005) Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest. *Ecoscience*, **12**, 151–160.
- Johnson EA (1992) *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest*. Cambridge University Press, Cambridge.
- Jurgensen MF, Larsen MJ, Spano SD, Harvey AE, Gale MR (1984) Nitrogen-fixation associated with increased wood decay in Douglas-Fir residue. *Forest Science*, **30**, 1038–1044.
- Kahl T (2008) *Carbon Transport from Deadwood to the Soil* [In German]. PhD Thesis, Faculty of Forestry and Environmental Sciences, University Freiburg, Freiburg, Germany, 109 pp. <http://www.freidok.uni-freiburg.de/volltexte/5522/>.
- Kajimoto T, Matsuura Y, Osawa A, Prokushkin A, Sofronov M, Abaimov A (2003) Root system development of *Larix gmelinii* trees affected by micro-scale conditions of permafrost soils in central Siberia. *Plant and Soil*, **255**, 281–292.
- Kandola BK, Horrocks AR, Price D, Coleman GV (1996) Flame-retardant treatments of cellulose and their influence on the mechanism of cellulose pyrolysis. *Polymer Reviews*, **C36**, 721–794.
- Kirk TK, Farrell RL (1987) Enzymatic combustion – the microbial degradation of lignin. *Annual Review of Microbiology*, **41**, 465–505.
- Kollmann FFP, Cote WA (1984) *Principles of Wood Science and Technology*, Vol. I. Solid Wood, Berlin.
- Krinner G, Viovy N, de Noblet-Ducoudré N *et al.* (2005) A dynamic global vegetation model for studies of the coupled atmosphere–biosphere system. *Global Biogeochemical Cycles*, **19**, 1–33.
- Kuehne C, Donath C, Muller-Using SI, Bartsch N (2008) Nutrient fluxes via leaching from coarse woody debris in a *Fagus sylvatica* forest in the Solling Mountains, Germany. *Canadian Journal of Forest Research*, **38**, 2405–2413.
- Large M, Braggins J (2004) *Tree Ferns*. Timber Press, Portland.
- Liers C, Ullrich R, Steffen KT, Hatakka A, Hofrichter M (2006) Mineralization of C-14-labelled synthetic lignin and extracellular enzyme activities of the wood-colonizing ascomycetes *Xylaria hypoxylon* and *Xylaria polymorpha*. *Applied Microbiology and Biotechnology*, **69**, 573–579.
- Liski J, Palosuo T, Peltoniemi M, Sievanen R (2005) Carbon and decomposition model Yasso for forest soils. *Ecological Modelling*, **189**, 168–182.
- Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Global Change Biology*, **13**, 2089–2109.
- Logan KJ, Thomas BA (1985) Distribution of lignin derivatives in plants. *New Phytologist*, **99**, 571–585.
- Luyssaert S, Inglima I, Jung M *et al.* (2007) CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, **13**, 2509–2537.

- Lynd LR, Weimer PJ, van Zyl WH, Pretorius IS (2002) Microbial cellulose utilization: fundamentals and biotechnology. *Microbiology and Molecular Biology Reviews*, **66**, 506–577.
- Mackensen J, Bauhus J, Webber E (2003) Decomposition rates of coarse woody debris – a review with particular emphasis on Australian tree species. *Australian Journal of Botany*, **51**, 27–37.
- Maherali H, DeLucia EH (2000) Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiology*, **20**, 859–867.
- Malhi Y, Baker TR, Phillips OL *et al.* (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 563–591.
- Martin T, Ogden J (2006) Wind damage and response in New Zealand forests: a review. *New Zealand Journal of Ecology*, **30**, 295–310.
- Martinez AT, Speranza M, Ruiz-Duenas FJ *et al.* (2005) Biodegradation of lignocelluloses: microbial chemical, and enzymatic aspects of the fungal attack of lignin. *International Microbiology*, **8**, 195–204.
- Martius C (1994) Diversity and ecology of termites in Amazonian forests. *Pedobiologia*, **38**, 407–428.
- McCulloh KA, Sperry JS (2005) Patterns in hydraulic architecture and their implications for transport efficiency. *Tree Physiology*, **25**, 257–267.
- McGuire A, Melillo J, Joyce L, Kicklighter D, Grace A, Moore B III, Vorosmarty C (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochemical Cycles*, **6**, 101–124.
- McGuire AD, Chapin FS, Walsh JE, Wirth C (2006) Integrated regional changes in Arctic climate feedbacks: implications for the global climate system. *Annual Review of Environment and Resources*, **31**, 61–91.
- Meinzer FC, James SA, Goldstein G, Woodruff D (2003) Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant Cell and Environment*, **26**, 1147–1155.
- Milla R, Castro-Diez P, Maestro-Martinez M, Montserrat-Marti G (2005) Relationships between phenology and the remobilization of nitrogen, phosphorus and potassium in branches of eight Mediterranean evergreens. *New Phytologist*, **168**, 167–178.
- Milosavljevic I, Oja V, Suuberg EM (1996) Thermal effects in cellulose pyrolysis: relationship to char-forming processes. *Industrial and Engineering Chemistry Research*, **35**, 653–662.
- Moorcroft PR, Hurtt GC, Pacala SW (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–585.
- Morrow A, Dute R (1998) Developmental and structure of pit membranes in the rhizome of the woody fern *Botrychium dissectum*. *IAWA Journal*, **19**, 429–441.
- Nishimura TB (2005) Tree characteristics related to stem breakage of *Picea glehnii* and *Abies sachalinensis*. *Forest Ecology and Management*, **215**, 295–306.
- Ohkuma M (2003) Termite symbiotic systems: efficient bio-recycling of lignocellulose. *Applied Microbiology and Biotechnology*, **61**, 1–9.
- Pak BC, Langenfelds RL, Young SA *et al.* (2003) Measurements of biomass burning influences in the troposphere over southeast Australia during the SAFARI 2000 dry season campaign. *Journal of Geophysical Research*, **108**, 8480.
- Parton W, Silver WL, Burke IC *et al.* (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, **315**, 361–364.
- Parton WJ, Stewart JWB, Cole CV (1988) Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry*, **5**, 109–131.
- Peterson CJ (2007) Consistent influence of tree diameter and species on damage in nine eastern North American tornado blowdowns. *Forest Ecology and Management*, **250**, 96–108.
- Polomski J, Kuhn N (2001) Root habitus and wind stability of trees. *Forstwissenschaftliches Centralblatt*, **120**, 303–317.
- Preston CM, Bhatti JS, Flanagan LB, Norris C (2006a) Stocks, chemistry, and sensitivity to climate change of dead organic matter along the Canadian boreal forest transect case study. *Climatic Change*, **74**, 223–251.
- Preston CM, Schmidt MWI (2006) Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences*, **3**, 397–420.
- Preston CM, Trofymow JA, Niu J, Fyfe CA (1998) ¹³CPMAS-NMR spectroscopy and chemical analysis of coarse woody debris in coastal forests of Vancouver Island. *Forest Ecology and Management*, **111**, 51–68.
- Preston KA, Cornwell WK, DeNoyer JL (2006b) Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist*, **170**, 807–818.
- Qualls RG, Haines BL (1991) Fluxes of dissolved organic nutrients and humic substances in a deciduous forest. *Ecology*, **72**, 254–266.
- Randerson JT, Van de Werf GR, Collatz GJ *et al.* (2005) Fire emissions from C₃ and C₄ vegetation and their influence on interannual variability of atmospheric CO₂ and δ¹³CO₂. *Global Biogeochemical Cycles*, **19**, GB2019.
- Reyes-Chilpa R, Jimenez-Estrada M, Estrada-Muniz E (1997) Antifungal xanthenes from *Calophyllum brasiliensis* heartwood. *Journal of Chemical Ecology*, **23**, 1901–1911.
- Richards GN, Zheng G (1991) Influence of metal ions and of salts on products of pyrolysis of wood: applications to thermochemical processing of newsprint and biomass. *Journal of Analytical and Applied Pyrolysis*, **21**, 133–146.
- Rock J, Badeck FW, Harmon ME (2008) Estimating decomposition rate constants for European tree species from literature sources. *European Journal of Forest Research*, **127**, 301–313.
- Roderick ML, Berry SL (2001) Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water. *New Phytologist*, **149**, 473–485.
- Romberger JA, Hejnowicz Z, Hill JF (2004) *Plant Structure: Function and Development: A Treatise on Anatomy and Vegetative Development, with Special Reference to Woody Plants*. Blackburn Press, Caldwell, NJ.
- Rothermel RC (1983) *How to Predict the Spread and Intensity of Forest and Range Fires*. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, p. 161.
- Rowell RM (2005) *Handbook of Wood Chemistry and Wood Composites*. CRC Press, Boca Raton, FL.

- Runkle J (2000) Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology*, **81**, 554–567.
- Running SW, Gower ST (1991) FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology*, **9**, 147–160.
- Sandved KB, Prance GT, Prance AE (1993) *Bark: the Formation, Characteristics, and Uses of Bark around the World*. Timber Press, Portland, OR.
- Scheffer TC, Cowling EB (1966) Natural resistance of wood to microbial deterioration. *Annual Review of Phytopathology*, **14**, 147–170.
- Scheffrahn RH (1991) Allelochemical resistance of wood to termites. *Sociobiology*, **19**, 257–281.
- Schowalter TD, Zhang YL, Sabin TE (1998) Decomposition and nutrient dynamics of oak *Quercus* spp. logs after five years of decomposition. *Ecography*, **21**, 3–10.
- Schultz TP, Nicholas DD (2000) Naturally durable heartwood: evidence for a proposed dual defensive function of the extractives. *Phytochemistry*, **54**, 47–52.
- Schutz JP, Gotz M, Schmid W, Mandallaz D (2006) Vulnerability of spruce (*Picea abies*) and beech (*Fagus sylvatica*) forest stands to storms and consequences for silviculture. *European Journal of Forest Research*, **125**, 291–302.
- Schuurman G (2005) Decomposition rates and termite assemblage composition in semiarid Africa. *Ecology*, **86**, 1236–1249.
- Schwilk DW (2003) Flammability is a niche construction trait: canopy architecture affects fire intensity. *American Naturalist*, **162**, 725–733.
- Schwilk DW, Ackerly DD (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos*, **94**, 326–336.
- Shevliakova E, Pacala SW, Malyshev S *et al.* (in press). Carbon cycling under 300 years of land-use change: the importance of the secondary vegetation sink. *Global Biogeochemical Cycles*.
- Sitch S, Smith B, Prentice IC *et al.* (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.
- Sjöström E (1993) *Wood Chemistry: Fundamentals and Applications*, 2nd edn. Academic Press, San Diego.
- Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography*, **10**, 621–637.
- Smithwick EAH, Harmon ME, Domingo JB (2007) Changing temporal patterns of forest carbon stores and net ecosystem carbon balance: the stand to landscape transformation. *Landscape Ecology*, **22**, 77–94.
- Songwe NC, Okali DUU, Fasehun FE (1995) Litter decomposition and nutrient release in a tropical rain forest, southern Bakundu Forest Reserve, Cameroon. *Journal of Tropical Ecology*, **11**, 333–350.
- Spears JDH, Lajtha K (2004) The imprint of coarse woody debris on soil chemistry in the western Oregon Cascades. *Biogeochemistry*, **71**, 163–175.
- Sperry J, Hacke U, Pittermann J (2006) Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany*, **93**, 1490–1500.
- Sperry JS, Meinzer FC, McCulloh KA (2008) Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant Cell and Environment*, **31**, 632–645.
- Stamm L (2006) *Measuring and Modelling Coarse Woody Debris in Tall Wet Eucalypt Forest in Southern Tasmania*. University of Tasmania, Hobart, p. 191.
- Sterner RW, Elser JJ (2002) *Ecological Stoichiometry: the Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.
- Stevens PF (2001-) Angiosperm Phylogeny Website Version 8, June 2007. Available at <http://www.mobot.org/MOBOT/research/APweb/>. (accessed January 2008).
- Suding KN, Lavorel S, Chapin FS *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.
- Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, **94**, 451–459.
- Takamura K, Kirton LG (1999) Effects of termite exclusion on decay of a high-density wood in tropical rain forests of Peninsular Malaysia. *Pedobiologia*, **43**, 289–296.
- ten Have R, Teunissen PJM (2001) Oxidative mechanisms involved in lignin degradation by white-rot fungi. *Chemical Reviews*, **101**, 3397–3413.
- Thornton PE (1998) *Regional Ecosystem Simulation: Combining Surface- and Satellite-Based Observations to Study Linkages between Terrestrial Energy and Mass Budgets*. School of Forestry, University of Montana, Missoula p. 280.
- Tinker DB, Knight DH (2000) Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems*, **3**, 472–483.
- Tokuda G, Watanabe H (2007) Hidden cellulases in termites: revision of an old hypothesis. *Biology Letters*, **3**, 336–339.
- Tyree MT, Zimmermann MH (2002) *Xylem Structure and the Ascent of Sap*. Springer, Berlin.
- Van de Werf GR, Randerson JT, Giglio L, Collatz GJ, Kasibhatla P, Arellano AFJ (2006) Interannual variability in global biomass burning emissions from 1997 to 2004. *Atmospheric Chemistry and Physics*, **6**, 3423–3441.
- van der Wal A, de Boer W, Smant W, van Veen JA (2007) Initial decay of woody fragments in soil is influenced by size, vertical position, nitrogen availability and soil origin. *Plant and Soil*, **301**, 189–201.
- van Gelder HA, Poorter L, Sterck FJ (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*, **171**, 367–378.
- Vaucher H, Eckenwalder JE (2003) *Tree Bark: A Color Guide*. Timber Press, Portland.
- Ward DE, Susott RA, Kauffman JB *et al.* (1992) Smoke and fire characteristics for cerrado and deforestation burns in Brazil: BASE-B experiment. *Journal of Geophysical Research*, **97**, 14601–14619.
- Watanabe Y, Mihara R, Mitsunaga T, Yoshimura T (2005) Termite repellent sesquiterpenoids from *Callitris glaucophylla* heartwood. *Journal of Wood Science*, **51**, 514–519.

- Weedon JT, Cornwell WK, Cornelissen JHC, Zanne A, Wirth C, Coomes D (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters*, **12**, 45–56.
- Wells JM, Boddy L (1995) Effect of temperature on wood decay and translocation of soil-derived phosphorus in mycelial cord systems. *New Phytologist*, **129**, 289–297.
- Wilson B, McComb B (2005) Dynamics of dead wood over 20 years in a New England oak forest. *Canadian Journal of Forest Research*, **35**, 682–692.
- Wirth C, Schulze E-D, Lühker B *et al.* (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant and Soil*, **242**, 41–63.
- Woldendorp G, Keenan RJ, Barry S, Spencer RD (2004) Analysis of sampling methods for coarse woody debris. *Forest Ecology and Management*, **198**, 133–148.
- Wood TG, Sands WA (1978) The role of termites in ecosystems. In: *Production Ecology of Ants and Termites* (ed. Brian MV), pp. 245–292. Cambridge University Press, Cambridge.
- Worrall JJ, Anagnost SE, Zabel RA (1997) Comparison of wood decay among diverse lignicolous fungi. *Mycologia*, **89**, 199–219.
- Yamada A, Inoue T, Wiwatwitaya D, Ohkuma M, Kudo T, Sugimoto A (2006) Nitrogen fixation by termites in tropical forests, Thailand. *Ecosystems*, **9**, 75–83.
- Yarmishko VT, Dem'yanov VA (1983) Structure of the root systems of woody plants in the mountains of northern Siberia, USSR. *Botanicheskii Zhurnal*, **68**, 1225–1235.
- Yin XW (1999) The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. *Oecologia*, **121**, 81–98.
- Zabel RA, Morrell JJ (1992) *Wood Microbiology – Decay and Its Prevention*. Academic Press, San Diego.

Supporting Information

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

Appendix S1. Wood chemistry data compilation methods and citations.

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