Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities

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ARTICLE INFO

ABSTRACT

Deadwood decay is an important ecosystem process in forest ecosystems, but the relative contribution of specific wood properties of tree species, activities of wood-degrading enzymes, and decomposer communities such as fungi and insects is unclear. We ask whether wood properties, in particular differences between angiosperms and gymnosperms, and organismic diversity of colonizers contribute to wood decomposition. To test this, we exposed deadwood logs of 13 tree species, covering four gymnosperms and nine angiosperm species, in 30 plots under different forest management in three regions in Germany. After a decomposition time of 6.5 years *Carpinus betulus* and *Fagus sylvatica* showed the highest decay rates. We found a positive correlation of decay rate with enzyme activities, chemical wood properties (S, K concentration) and organismic diversity, while, heartwood character, lignin content, extractive concentration and phenol content were negatively correlated with decay rate across all 13 tree species. By applying a multi-model inference approach we found that the activity of the wood-degrading enzymes laccase and endocellulase, beetle diversity, heartwood presence, wood ray height and fungal diversity were the most important predictor variables for wood decay. Although we were not able to identify direct cause and effect relations by our approach, we conclude that enzyme activity and organismic diversity are the main drivers of wood decay rate, which greatly differed among tree species. Maintaining high tree species diversity will therefore result in high structural deadwood diversity in terms of decay rate and decay stage.

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1. Introduction

Deadwood is known to be an important structural component of forests (Bauhus et al., 2009) that influences a large number of ecosystem functions (Harmon et al., 1986; Cornwell et al., 2009)

and is a critical resource for wood-dwelling organisms (Lonsdale et al., 2008; Rondeux and Sanchez, 2010; Stokland et al., 2012).

The rate of deadwood decay, as a combination of biological respiration, leaching and fragmentation (Harmon et al., 1986), is mainly the result of organismic activity (e.g. fungi, insects), determined by intrinsic (e.g. tree species properties) and environmental factors (e.g. temperature, moisture). In the early phase of decay, biological respiration (i.e. mineralization of wood components to CO_2) is the main process, while leaching only accounts for about 1–2% of mass loss (Kahl, 2008; Bantle et al., 2014). Fragmentation can also cause a substantial mass loss of deadwood, e.g. 18–30% of decomposition rates over the first 18 years in some European tree species (Herrmann et al., 2015), and it may become even more important in the late phase of decomposition (up to 40%; Harmon et al., 1986).

Decay rates for common European tree species have been well documented for different climatic regions (Pietsch et al., 2014). First estimates were reported for *Quercus* spp., *Fraxinus excelsior*, *Betula* spp. and *Corylus avellana* (Swift et al., 1976; Christensen, 1977) already in the 1970s. However, decay rates for less abundant tree species such as *Carpinus betulus*, *Prunus avium* or *Tilia* spp. have not been quantified.

Estimates on decay rates are often based on a chronosequence approach, where *in-situ* deadwood is sampled of different times since death and compared. This approach has a sampling bias, due to the fact that deadwood with low decay rates is more likely to be sampled than deadwood with high decay rates, which may have already decayed completely at the time of observation (Kruys et al., 2002). This may result in an underestimation of deadwood decay rates. To quantify true decay rates, these should be measured during the entire time course of wood decay. An unbiased estimation of decay rates can either be achieved by resampling of sites that include all recently killed trees, or by experiments that place deadwood logs in forests. Such site-based multi-species studies on decay rates including angiosperms and gymnosperms are, however, still largely lacking (Weedon et al., 2009).

Decay rates of different tree species could be largely affected by functional group or species-specific wood traits. A meta-analysis of Weedon et al. (2009) showed that gymnosperms generally tend to have lower decay rates than angiosperms. In gymnosperms, solvent extractable organic compounds (extractives) comprise mainly terpenes and their derivatives, which slow down fungal growth and degradation activity (Dix and Webster, 1995; Pearce, 1996). In contrast, in angiosperms the chemical composition of extractives is more diverse, reaching from resin-like materials of carbohydrate gum in cherry (Pearce, 1996), which may not affect decay, to phenolic compounds (e.g. quercitin) and tannins in oak, which inhibit fungal growth (Hart and Hillis, 1972; Aloui et al., 2004). Furthermore, the lignin of gymnosperms is more difficult to oxidize compared to that of angiosperms, since it consists to more than 90% of guaiacyl moieties, compared to 0–33% in angiosperm lignin. The lignin of angiosperms contains a higher proportion of sinapyl moieties that degrades more easily (Brunow, 2001; Higuchi, 2006). Guaiacyl units make the lignin of gymnosperms particularly compact, which impedes enzymatic attack in general (Hatakka and Hammel, 2010).

Within angiosperms, wood traits such as phosphorus and nitrogen content, and low C:N ratio are positively correlated with decay rates (Weedon et al., 2009). It is also well known (EN350-2, 1994) that tree species with distinct heartwood (e.g. *Quercus* spp.) tend to have higher resistance against wood decaying fungi. The content of extractives, such as tannins and terpenoids/resins, in heartwood is often higher than in sapwood and the extracts from heartwood are usually more toxic (Scheffer, 1966; Hillis, 1999; Gierlinger et al., 2004).

Furthermore differences in the presence of organisms and their activity might affect wood decay. A high diversity of saproxylic fungi and beetle species in logs of different tree species have been shown in previous studies (Baber et al., 2016; Gossner et al., 2016). In wood decomposition mediated by fungi, the main secreted enzymes are oxidoreductases modifying lignin via radical formation with the help of dioxygen (laccase) or hydrogen peroxide (several peroxidases), and diverse glycoside hydrolases, which hydrolytically cleave the major polysaccharides (cellulose, hemicelluloses) to sugars (Hatakka and Hammel, 2010; Kellner et al., 2014; Arnstadt et al., 2016a; Noll et al., 2016). While substantial lignin decomposition is exclusively mediated by white-rot basidiomycetes possessing high-redox potential peroxidases (i.e. class II manganese and lignin peroxidases, Floudas et al., 2012), cellulose and hemicelluloses can be disintegrated by all wood-decomposing fungi (white-, brown- and soft-rot fungi), as well as by specialized bacteria. The resulting sugars, e.g. cellobiose, glucose, xylose, mannose, and arabinose, serve as carbon and energy source (Riley et al., 2014). Against this background, the activities of laccase, manganese and general peroxidases can be used as proxy for lignin attack. The same is true for *endo*-1,4-β-glucanase and *endo*-1,4-β-xylanase, which mediate the first step in the breakdown of the polysaccharide backbone by forming oligo-, di- and monosaccharides (Kögel-Knabner, 2002) representing the enzymatic polysaccharide disintegration. Despite the importance of these enzymes for wood decomposition, their relation to decay rates of deadwood has never been studied. Only few publications have so far analyzed enzymes in deadwood (Valaskova et al., 2009; Větrovský et al., 2011; van der Wal et al., 2015; Arnstadt et al., 2016a; Baldrian et al., 2016; Noll et al., 2016; Purahong et al., 2016).

Differences in fungal species identity and fungal communities can cause distinct differences in decay rates (Boddy, 2001; Kahl et al., 2015). However, to date no consistent relationship between deadwood decomposition and fungal decomposer diversity has been demonstrated (van der Wal et al., 2013). It has been shown that decay rates can be either positively (Setälä and McLean, 2004; Tiunov and Scheu, 2005; Toljander et al., 2006; Valentín et al., 2014; Kahl et al., 2015) or negatively (Fukami et al., 2010) correlated with fungal species richness. Based on the quantification of fungal operational taxonomic units (OTU), Hoppe et al. (2015) found no correlation between total richness (using molecular NGS 454 data) and wood decomposition rate in both coniferous (*Picea abies*) and deciduous (*Fagus sylvatica*) deadwood. Admittedly, there is an undeniable relationship between fungal community composition and wood decomposition. The fungal assembly history (Fukami et al., 2010), the presence of species with extraordinary decomposition activities (Lindner et al., 2011; Kubartová et al., 2012) and the environmental conditions (Renvall, 1995; Høiland and Bendiksen, 1996) can determine the strength of this relationship. Van der Wal et al. (2015) showed that the most important factors explaining variation in wood decay rates can change over time and the strength of competitive interactions between fungi may level off with increased wood decay. This study furthermore showed that wood moisture content contributed especially to explain sapwood decay in early decay stages, whereas fungal community composition and species richness were the best predictors for mass loss in the later stages (van der Wal et al., 2015).

Insects also play an important role in the wood decomposition process. Based on a meta-analysis, Ulyshen (2016) estimates the contributions of invertebrates to wood decomposition to account for 10–20%. He suggests four main underlying mechanisms: (1) enzymatic digestion by endogenous enzymes (Watanabe and Tokuda, 2001, 2010) as well as by enzymes produced by endo-(gut microbes; e.g. Suh et al., 2005) and ectosymbionts (e.g. fungi